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# ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS

*of the*

NEW YORK ZOOLOGICAL SOCIETY

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# ZOOLOGICA

## SCIENTIFIC CONTRIBUTIONS

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## NEW YORK ZOOLOGICAL SOCIETY

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### 1.

## Social and Respiratory Behavior of Large Tarpon.

C. M. BREDER, JR.

*New York Zoological Society*

(Text-figure 1).

### INTRODUCTION.

This report is in the nature of a continuation of the studies of Shlaifer & Breder (1940) and was made incidental to other work to be reported elsewhere. For these latter purposes five tarpon were confined in a pen built of slats 13'2"  $\times$  7'0"  $\times$  5'8" deep. This was submerged in the artificial channel serving as a means of egress from Palmetto Key, Florida. The five fish averaged about five feet in standard length. The smallest, estimated at four feet in length, was a male in a ripe condition; the remaining four were females that were nearly ripe. They were caught and placed in the pen by Marshall B. Bishop late in May. The counts on their rises for respiratory purposes began on June 11 as given in Table I. In this the writer was assisted by Mr. Ben Dontzin who made readings Nos. 10 to 22. One reading was made simultaneously with a similar reading in the tarpon pool described in Shlaifer & Breder (1940). It is noted in Table I as P1. Since these authors have already described the respiratory behavior of immature and small tarpon it was thought desirable that some comparable measurements be made on the adult, sexually mature individuals.

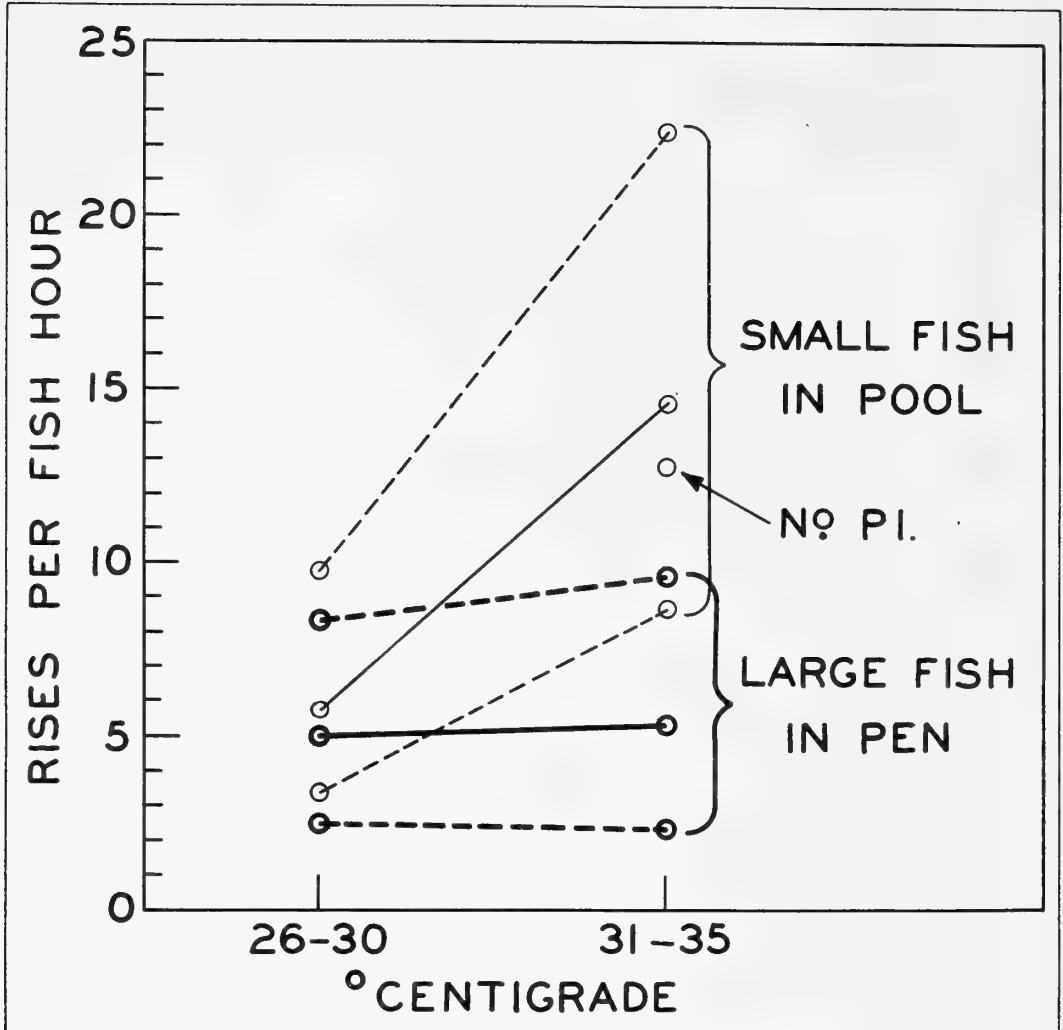
The methods employed have already been set forth by Shlaifer & Breder (1940), and Shlaifer (1941) has shown that atmospheric respiration is obligatory on this species.

### RESULTS.

The results obtained are clearly comparable with those gotten on the smaller fish. There are certain noteworthy differences, however, which include chiefly that the fishes of these larger sizes do not rise with quite the frequency of the smaller speci-

mens. If the number of rises per hour is referred to the temperature range, Table II, and compared with the earlier data on smaller fishes, it will be noted that in the 26°-30° range the figures are almost identical but slightly lower for the larger fish, while in the 31°-35° range the larger fish are definitely much lower than the smaller. This may well have to do with the environment rather than the size of fish. The large fish were held in a pen through which circulated tidal waters, whereas the small fish were confined to a stagnant pool in which gaseous exchange occurred only through the air-water interface as there was no continuous replacement by flow. A comparison of these data are given in Text-figure 1.

It is evident from observations in both Boca Grande and Captiva Passes that tarpon tend to rise for air in groups. This social aspect of the respiratory need for air was discussed at length for the smaller sizes by Shlaifer & Breder (1940). Similar data for large fish in a pen, handled in identical fashion, is given in Table III. It will be noted that here there is relatively little social influence being shown. It is much less than the average shown for small fish in various-sized bodies of water. These authors found that the larger the body of water the less the imitation, presumably due to the greater chance separation of the fishes. On this basis the present large fish should show a marked amount of imitation. That they showed less suggests the presence of some other factor. It is to be noted that the social attitude of the small fish in the pool (P1) is comparable to readings taken in it a year earlier and not with the large penned fish. These fish were approaching the spawning condition which well may have an effect on their social attitude. Later it was found on examination



Text-fig. 1. Comparison of respiratory activity of large and small tarpon showing both means and extremes. Data on small fish from Schlaifer & Breder (1940).

that these fish were actually reabsorbing their eggs under the apparent influence of captivity. They were, for their size, relatively closely confined, but not any more so than the small fish studied in aquaria which showed the greatest amount of imitation.

A more detailed comparison of this influence in large and small tarpon is impossible for the present as the effects of temperature and oxygen content at least would have to be much better understood before an attempted explanation of the effect on respiration of absolute size of fish or its condition in regard to spawning time could be ascertained.

As may be noted from Table I, the variation in respiratory activity was marked by abrupt changes in rises per hour that could

not be associated with temperature, time of day or any other ascertainable influence.

As a further continuation of the work of Schlaifer & Breder (1940) observations were made on a single tarpon of 35.6 cm. in standard length in the laboratory pool. These data were taken by Mr. Ben Dontzin. Condensed, they appear as follows:

Date	Time	°C	Rises per hour
12/26/41	5:00 p.m.	—	2
12/27/41	11:15 a.m.	26.5	2
12/27/41	5:15 p.m.	23.5	4
12/28/41	10:45 a.m.	27.0	1
12/29/41	11:10 a.m.	29.0	6
12/30/41	1:15 p.m.	26.0	5

Each period of observation continued for an hour beginning with the time indicated.

The data is presented as in Table VII of Shlaifer & Breder (1940). It agrees well with their work and in reference to their temperature comparisons stands as follows:

Temperature in 5° intervals centigrade.		
Rises per fish hour	21-25	26-30
Present data		
Mean	4	3.5
Maximum	—	6
Minimum	—	1
Shlaifer & Breder (1940)		
Mean	4.8	5.7
Maximum	10.4	9.6
Minimum	1.6	3.3

It thus develops that this single fish rose to breathe with slightly less frequency than did those in the larger groups (3 to 5) previ-

ously studied. This is in keeping with expectation on a social basis. Although this data is scant it can, in reference to the earlier work, be considered as confirmatory. The pool contained a large number of small *Mugil* which were not present during the earlier work, but which apparently have little if any effect on respiratory behavior.

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1940. Social and Respiratory Behavior of Small Tarpon. *Zoologica*, 25(30): 493-512.

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TABLE I.  
Respiratory Activity of Adult Tarpon in Confinement.

(5 mature fish in a live car). (One hour observation periods).								
No.	Date	Time	°C	Rises	Rises per Fish Hour	Greatest Time Between Rises	% of Minutes with no Rises All Per Fish	
1	6/11	1:45	33.8	18	3.6	5:33	70.0	14.0
2	6/12	2:00	33.8	16	3.2	6:03	73.3	14.6
3	6/13	6:15	32.9	42	8.4	4:40	48.3	9.6
4	6/14	1:45	33.6	30	6.0	4:02	58.3	11.6
5	6/14	7:00	32.2	29	5.8	6:26	61.6	12.3
6	6/15	2:30	33.6	36	7.2	3:23	48.3	9.6
7	6/17	1:30	33.8	23	4.6	6:29	65.0	13.0
8	6/18	1:30	31.1	18	3.6	5:13	71.6	14.3
9	6/24	1:45	31.7	20	4.0	8:30	73.3	14.6
10	6/25	10:00	31.1	40	8.0	4:02	53.3	10.6
11	6/25	2:00	32.9	12	2.4	8:39	81.6	16.3
12	6/25	6:30	31.7	24	4.8	6:50	68.3	13.6
13	6/26	10:30	31.7	47	9.4	4:42	51.6	10.3
14	6/26	2:00	33.8	18	3.6	6:44	70.0	14.0
15	6/26	6:45	32.2	18	3.6	7:29	63.3	12.6
16	6/27	11:30	31.1	46	9.2	4:37	50.0	10.0
17	6/27	7:00	30.0	21	4.2	5:47	68.3	15.6
18	6/29	10:00	30.0	41	8.2	5:25	53.3	10.6
19	6/29	6:00	31.1	20	4.0	4:43	71.6	14.3
20	6/30	6:30	30.5	11	2.2	19:35	81.6	16.3
21	7/2	9:30	30.0	26	5.2	7:13	71.6	14.3
22	7/2	7:00	29.4	12	2.4	9:06	81.6	16.3
Mean			31.9+	26—	5.2—	6:36—	65.3—	13.1+
Maximum			33.8	47	9.4	19:35	73.3	16.3
Minimum			29.4	11	2.2	3:23	48.3	9.6
Simultaneous reading with No. 10 above of four immature fish in a land-locked pool.								
P1	6/25	10:00	33.9	51	12.75	3:17	40.0	8.0

TABLE II.

Respiration in Regard to Temperature Compared with that of Small Fish.

Rises per Fish Hour	Temperature in 5° intervals centigrade				
	16-20	21-25	26-30	31-35	36-40
Large fish in pen	—	—	4.2	3.6	8.4
	—	—	8.2	4.0	6.0
	—	—	5.2	8.0	5.8
	—	—	2.4	4.8	7.2
	—	—	—	9.4	4.6
	—	—	—	9.2	2.4
	—	—	—	4.0	3.6
	—	—	—	2.2	3.6
	—	—	—	3.6	—
	—	—	—	3.2	—
Mean	—	—	5.0	5.2	—
Maximum	—	—	8.2	9.4	—
Minimum	—	—	2.4	2.2	—
Small fish (From Shlaifer & Breder, 1940)					
Mean	0.8	4.8	5.7	14.5	10.0
Maximum	0.8	10.4	9.6	22.3	10.8
Minimum	0.8	1.6	3.3	8.6	9.0

TABLE III.

Fishes Rising in Groups by Percent of Total.

No.	1	2	3	4	5	Total
1	100	0	0	0	0	18
2	100	0	0	0	0	16
3	100	0	0	0	0	42
4	93.5	6.65	0	0	0	30
5	93.1	6.9	0	0	0	29
6	100	0	0	0	0	36
7	100	0	0	0	0	23
8	100	0	0	0	0	18
9	100	0	0	0	0	20
10	95	5.0	0	0	0	40
11	100	0	0	0	0	12
12	100	0	0	0	0	24
13	100	0	0	0	0	47
14	100	0	0	0	0	18
15	100	0	0	0	0	18
16	95.65	4.35	0	0	0	46
17	100	0	0	0	0	21
18	100	0	0	0	0	41
19	100	0	0	0	0	21
20	100	0	0	0	0	11
21	100	0	0	0	0	26
22	100	0	0	0	0	12
Average	99.0—	1.0+	0	0	0	26—
Maximum	100	6.9	0	0	0	47
Minimum	93.1	0	0	0	0	11

Simultaneous reading with No. 10 above of 4 immature fish in a landlocked pool.

P1	80.5	7.85	11.65	0	—	51
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## 2.

**Tetanus in an Elephant (*Elephas maximus*).**

LEONARD J. GOSS

*Veterinarian, New York Zoological Park.*

An Indian elephant was received at the New York Zoological Park on October 8, 1940, at the approximate age of eight years. It weighed 2,100 pounds. On May 2, 1941, the elephant's keeper noticed that the animal was unable to open its mouth. Two and one-half hours later, examination revealed the following: jaws tightly closed; temperature, 98.6°; hypersensitiveness to sound; prolapsing of the nictitating membranes; and erection of the tail (poker tail) when the animal was touched or excited. A diagnosis of tetanus was made. There were numerous small cracks on the feet around the toenails and healing superficial wounds in the skin at the base of the ears. None of these wounds was sensitive to palpation or was the type of wound usually associated with tetanus infection.

After examination, 100,000 units of tetanus antitoxin were given subcutaneously: 50,000 on each side of the neck.

The next day, the animal seemed less sensitive to noise and palpation and was able to open its mouth just enough to admit a one-inch stomach tube. It drank water when the tube was placed in the mouth and water allowed to run slowly. The animal attempted to eat but the mouth could not be opened sufficiently to admit food. It was felt that improvement was sufficient and no antitoxin was given on this day. Considerable edema was present in the neck region where the antitoxin had been administered.

The morning of the third day, May 4, the animal was found broadside, in tetanic spasms. Two ounces of chloral hydrate as a 7% solution were given per rectum after manual removal of the fecal material. The spasms were relieved in twenty minutes and deep sleep occurred which persisted for two hours. During this time, 120,000 units of antitoxin were given and the patient again was examined for wounds which might account for the infection. This examination was not revealing. As the sleep wore off mild

spasms recurred and an additional 4 ounces of chloral hydrate were given per rectum. During the night the chloral hydrate anesthesia wore off but no spasms followed.

On May 5, the animal was unable to rise. Slings and a hoist were used to raise the patient to its feet; the mouth could be opened about one-third its normal opening. Sixty thousand units of antitoxin were given subcutaneously in the region of the flank and three loaves of bread made into small balls were placed in the mouth. These were swallowed with difficulty, followed by water from the hose held in the mouth. Stiffness of the legs was quite apparent, but the animal was capable of moving about slowly and was permitted outdoors all day. Constant unsuccessful attempts were made to eat grass and hay. In the afternoon a bran mash consisting of six quarts of bran in a bucket of water was given through a stomach tube held in the mouth. This was followed by three loaves of bread given in small balls.

On May 6, the condition of the animal was unchanged. She was kept quiet and fed in the manner previously described plus three dozen bananas and two pounds of sugar. This food was given daily and the condition remained the same until May 9 when the stiffness of the legs became more pronounced and marked edema developed in the forelegs from the feet to the shoulders. Eighty thousand units of antitoxin were given. The quantity of bran was doubled to twelve quarts per day in addition to three dozen bananas, two pounds of sugar and three loaves of bread.

From May 9 to May 25, hand feeding was continued as usual and no change in condition occurred. By May 25 the animal had lost considerable weight and was down and unable to rise. She was assisted to her feet by the use of a hoist and was kept in slings and fed through a hose until June 4 when she began to eat hay and had complete use of her jaws.

Throughout the illness urine and fecal material were passed but in diminished quantities.

Several points of interest are apparent in this case:

1. No external wound could be found which might account for the infection.
2. Chloral hydrate is an effective anesthetic for elephants when given in

doses smaller than those required for horses of a similar weight.

3. 360,000 units of tetanus antitoxin were used in treating the patient.
4. It must be assumed that the infection was of alimentary origin, which is not improbable because of the habit of elephants of eating large quantities of dirt and refuse from the ground.

## 3.

**Descriptive Ecology of La Cueva Chica, with Especial Reference to the Blind Fish, *Anoptichthys*.**

C. M. BREDER, JR.

*New York Zoological Society.*

(Plates I-III; Text-figure 1).

## INTRODUCTION.

A blind cave-dwelling characin was described from the state of San Luis Potosi, Mexico, by Hubbs & Innes (1936) under the name *Anoptichthys jordani*. The original material had been collected by Señor Salvador Coronado that year, and sent in a living condition to Mr. C. B. Jordan of Texas, who in turn transmitted the material to Dr. Hubbs. Since then the fish has become established in small aquaria as a novelty. Nothing was recorded concerning the habitat of the form other than that mentioned by Hubbs & Innes (1936) and Hubbs (1938).

The New York Aquarium undertook the organization of a small expedition to study the nature of the environment of this cave. This trip, in March, 1940, described by Bridges (1940), occupied fifteen days actually spent in the cave. The present report contains the observational data obtained and as much ecological data as the field work yielded. A fuller discussion of the biological implications must wait on further laboratory work, which was in progress at the New York Aquarium, and has lately been transferred to the Department of Animal Behavior at the American Museum of Natural History.

It had been the original plan to have this translated into Spanish, edited by Señor Coronado and published in Mexico as a joint contribution. Due to inability to maintain satisfactory contact with Coronado, and rather than have the finished manuscript lie for an indeterminate period, it was decided to delay publication no longer.

The author takes this opportunity to thank Señor Coronado for his able assistance in the field. His energy, indefatigable efforts and general help went far toward the successful prosecution of our field work and we are grateful to Señor Antonio G. García, Jeffe del Departamento Tecnico de

la Direccion de Pesca é Industrias Maritimas, for releasing him from his ordinary duties in our behalf.

This paper was to have preceded the following documents: Hobbs (1941), Breder & Gresser (1941a, 1941b and 1941c). This proved impractical because of the delay alluded to above. The present contribution records the basic field data of the expedition, including the climatic, geologic and faunistic conditions as encountered in La Cueva Chica.

## GEOLOGY.

The accompanying map and vertical section of the cave, Text-figure 1, which has already appeared in Bridges (1940), gives a general idea of the cave. An inset gives the geographical location of the cave which is readily accessible from the concrete highway that runs from Laredo, Texas to Mexico City. All rock specimens have been examined by Dr. Horace E. Wood II and prove to be limestone formations of various types. The only exception to this is some litter on the floor of the cave which extends back to Pool No. 3. Presumably it actually goes further but is either covered with water or bat guano beyond that point. The litter itself consists of a wide variety of materials, mud, broken logs and water-worn stones and pebbles, some of which are conglomerates of reddish jade-like materials. These objects are carried in by means of rainy season torrents.

The entire region is honeycombed with sink-holes and caves of various sizes primarily formed by the solvent and eroding action of water. This water, heavily charged with calcium, has re-deposited materials to form stalactites, stalagmites and flow-stones, making typical cave structures. Apparently in La Cueva Chica both activities are going on simultaneously or alternately in different

places. The consequence is that there are many badly eroded structures, while a little distance from them are new ones in the early formative state. Broken chunks of rock clearly fall from the ceiling more or less regularly. Various types of stalactites, flow-stone and cup formations are all in evidence in the various photographs. There was also, in the higher places, a considerable amount of crystalline calcite, rhombic crystals, mostly blackish in color, and more or less amorphous masses with partly formed irregular crystals varying from yellow to tan.

Pool No. 1, well protected by rock walls and under a relatively low ceiling, was found to be covered with a fine dust, Plate I, Fig. 1. This was of a calcareous nature, checked by Dr. R. T. Cox spectrographically, perhaps crystalized on the walls as the water receded and then powdered off on the surface of the water. It was not found in the damper portions further from the cave mouth.

The region is one of hot springs as well as normal and cooler surface water. One such hot spring, El Bañito, is only three miles from the cave under consideration. These springs are heavily charged with sulphur and evidence of the complete lack of connection with such places by La Cueva Chica is the absence of sulphurous odors and the abundant life it contains. All other places examined showed no evidence of blind fishes, nor did the local people know of any other than in La Cueva Chica. Near the river just east of Pujal a deep hole has a number of lateral fissures. In places where light enters, normal *Platypoecilus* and *Astyanax* may be found but the cave waters proper were barren. This so-called "well" is believed to intercommunicate with La Cueva Chica. Various springs in the immediate vicinity show similar conditions, as does El Nilo, a cave from the mouth of which water flows, reversing sequences at La Cueva Chica.

Because of certain geological features of the general region and the interest in the possible effects on evolution of radioactive materials, tests were conducted on the presence of such emanations. Dr. M. D. Whittaker of the Department of Physics of New York University kindly undertook to make such tests on a series of water samples from each pool including evaporated concentrates. His findings were completely negative. Since, if radioactive material were present, they would surely appear in the ground waters, it is considered established that evolutionary activity in this cave proceeds without any such acceleration.

For a general discussion of the geology of the region, see Schuchert (1935) and Muir (1936). The accompanying photographs

show clearly the general nature of the formations. Still other photographs of the cave are given in Bridges (1940) and Dunton (1940).

#### WATER.

The chemical nature of the water of La Cueva Chica is shown in Table I. The analyses have been made by the Laboratory of the New York City Department of Water Supply through the courtesy of Mr. Herman Forster. These analyses show that the cave waters are high in nitrogen as compared with the river samples. The springs, as would be expected, are intermediate.

The chlorides, while variable, show no distinct trend from one type of water to another.

The hardness of the underground waters is clearly less than that of the surface streams, which in part at least probably accounts for the preference of the local people to caves for their water supply. On the other hand, the alkalinity tends to be higher in the caves than outside.

Phosphates are practically absent, being reported as "considerably less than .05 ppm  $\text{PO}_4$ ."

Sulphates, on the other hand, are high in the surface waters and in one of the hot springs. They are relatively low in the cave waters.

The water apparently feeds into Pool No. 1 or 2 through subterranean springs. The former is probably connected with the latter as is indicated in the map, Text-fig. 1. Pool No. 2 spills over into a running brook which widens in the area of the series of cups from which it runs into Pool No. 3. It drops into this over a nearly vertical plunge of about 25 feet. This flow continues on until the major bat roost is reached. Here there is a small waterfall from an overhanging shelf and further on another, in two streams down a mud slope to Pool No. 4. The water draining into Pool No. 4 is clearly of considerably greater volume than that leaving Pool No. 2. Consequently, it is to be interpreted that there are a considerable number of tributary additions along this length of the gallery. In fact, in many places there are to be seen wet and dripping places on the walls, showing the influx of additional water.

The water in all places is crystal clear, even in the far recesses of the cave where everything is floored with and the water surface covered by bat guano. The temperatures and pH readings are given in Table I. These both are remarkably uniform and no significant temperature differential could be noted between surface and bottom in depths up to twenty feet. An exception to this must be made in several readings of temperature in the small basins above Pool

TABLE I.  
Temperatures, Humidities and Water Analyses.

	P O O L S					L A C U E V A C H I C A					O T H E R L O C A L I T I E S				
	No. 1	No. 2		No. 3		Month Outside of Cave	Limit of Cave Daylight	Pool No. 2	Small Basins Above Pool No. 3	La Poza de la Virgen	Río Tampao	El Nilo	El Banito <sup>2</sup>		
		No. 1	No. 2	No. 3	No. 4										
Date (March 1940)	11	11	14	14	14	19	19	19	18	18	20	21	21	23	25
Air °C.	—	—	22.8	—	20.6	25.3	22.2	23.3	26.0	26.0	27.5	33.3	33.3	25.6	—
Rel. Humidity %	—	—	84	—	—	67	57	93	—	—	—	—	—	—	—
Water °C.	26.1-27.	26.1-27.2	26.71	—	—	—	—	—	23.5	24.0	25.0	27.8	29.4	22.2	32.8
pH	8.0	8.0	—	—	—	—	—	—	—	—	—	—	—	8.0	7.9

	C A V E W A T E R S			C O O L S P R I N G S			H O T S P R I N G S <sup>3</sup>			R I V E R S		
	La Cueva Chica Pool No. 2	Pool No. 3		Near Pujal	Between Pujal and Valles	La Poza de la Virgen	El Banito	Taniñul	El Banito	Río Tampao	Río Taniñul	
		No. 1	No. 2									
Date (March 1940)	14	19	23	15	21	20	25	29	25	20	29	
Albuminoid ammonia (p.p.m. Nitrogen)	.300	.260	.260	.180	.200	.480	.180	.260	.180	.120	.160	
Free ammonia (p.p.m. Nitrogen)	.480	.280	.160	.260	.480	.380	.340	.600	.340	.200	.220	
Nitrate (p.p.m. Nitrogen)	1.00	2.00	5.50	0.30	0.10	1.50	0.10	0.10	0.10	0.10	0.30	
Chlorine (p.p.m.)	4.0	8.0	5.0	9.0	8.0	20.0	7.0	188.0	7.0	11.0	4.0	
Hardness (p.p.m. Calcium Carbonate)	310	230	290	300	360	110	540	360	540	790	610	
Alkalinity (p.p.m. Calcium Carbonate)	282	218	234	282	310	76	286	318	286	134	246	
PO <sub>4</sub> (p.p.m.) <sup>3</sup>	nil.	nil.	nil.	nil.	nil.	nil.	nil.	nil.	nil.	nil.	nil.	
SO <sub>4</sub> (p.p.m.)	16	24	6.0	19	77	1.4	267	47	267	600	376	

Laboratory Analyses.

<sup>1</sup> At surface and at bottom (12').

<sup>2</sup> Sulphur water.

<sup>3</sup> Considerably less than .05 p.p.m. PO<sub>4</sub>.

No. 3. Here readings of 23.5, 24.0 and 25.0 were recorded. This seemed to be associated entirely with the speed of flow through a given cup, those receiving a good flow being substantially the temperature of the large pools, while those that were relatively stagnant varied, generally on the high side, presumably increasing in temperature because of the generally warmer cave atmosphere.

The entire temperature situation in this cave is apparently influenced by the proximity of the underlying magma. We are assured by Dr. H. E. Wood II that such temperatures could not be maintained in such a cavern on a basis of surface air and water temperatures alone.

During the rainy season it is impossible to enter the cave, according to local statements. When seen by us a completely dessicated stream bed led into the mouth of the cave. In addition to local statements there was much evidence that during the rainy season this stream becomes a roaring torrent, almost surely completely closing the cave mouth. The internal evidence of the cave supported this, and it would seem that the place fills with water with the possible exception of the high-vaulted chambers which may hold pockets of air at all times. Mud carried to high cavities in the wall gave evidence of this. A considerable formation of flow-stone steps is reached before Pool No. 1 is found, and were perfectly dry at the time of our visit.

Probably early in the season most of the action of the water is corrosive and attritional, while later with the water moving slowly with both solution and deposition going on, there is a tendency to build up more deposits of limestone, which process goes on throughout the dry season wherever water remains.

Locally the water is considered thoroughly potable and is much used by a nearby Indian village, inhabitants of which draw their water from Pools No. 1 and 2.

#### CAVE CLIMATE.

The climate of La Cueva Chica at the time of our visit was fairly static, but probably this cave varies considerably throughout the year in regard to temperature and humidity, at least much more so than most caves that have been reported on, partly because of its small size.

Since water enters the cave in great quantities for part of the year, it undoubtedly influences the temperature to a considerable extent, very likely tending to reduce it, since swollen, rainy-season streams are generally much cooler than other surface waters.

The ventilation of this cave is extremely limited. The only openings to the outside

that we could find were the entrance we used and a small crevice opening about two hundred feet away. This latter was detected only by reason of some smoke from photographic flares, used for the taking of motion pictures, finding its way out this small opening too narrow to pass a man. The behavior of smoke from these flares and the long time it hung in the chambers precluded the existence of any hidden crevice of importance. Also, the behavior of the bat colony indicated that they used the one major entrance only.

Although the air was oppressive and heavy, it was not unpleasant to smell until the area of the major bat roost was entered. Here it had the acrid, gagging characteristics generally associated with a sizeable bat colony.

Apparently the only change of air is that induced by weather changes, which "pump" air in or out, depending on the behavior of the barometric pressure. Added to this would be whatever dissolved gases invade or evade through the water surface to accumulate or be carried along to greater depths by the water flow. The daily flight of bats in and out no doubt also contributes to the agitation of the air, preventing any stratification.

Up to the first pool the direct effects of daily weather changes could be detected. That is, on dry days the walls would show condensed moisture where the damp air of the cave tended to cool when it made contact with the outer dry air. Here at such times the atmosphere of the entrance was refreshing, but beyond such a point, varying from day to day, it was consistently oppressive.

Data on temperature and humidity are given in Table I.

#### TERRESTRIAL ORGANISMS.

The only moderately large terrestrial animals that apparently dwell regularly in La Cueva Chica are the bats. These are exceedingly numerous, and while it was not the purpose of the expedition to study the bats, they were sufficiently conspicuous to warrant some remarks. When Dr. Myron Gordon entered the cave in 1939 as far as Pool No. 2, he found a good sized colony over that body of water. On our visit we did not encounter more than a few small groups of bats until the region marked on the map "minor bat colony" was reached. From here on bats were numerous, concentrated into two colonies, the second of which was immense.

The few specimens collected were kindly identified by Dr. J. E. Hill, of the American Museum of Natural History, as: *Artibeus jamaicensis* Leach, *Natalus mexicanus* Miller and *Mormoops megalophylla senicula* Rehn. Due to the inrush of water in the

rainy season these bats almost surely must vacate the cave for part of the year. *Micronycteris megalotis mexicanus* Miller was taken in El Nilo.

Mr. Marshall Bishop reported seeing some bats scamper high up the walls in true vampirine fashion. This, coupled with local accounts of vampire attacks on farm animals, sounded convincing, and the finding of droppings in El Nilo that looked very typical of vampire droppings, leads us to believe that they are actually dwelling in this region.

Aside from that of human beings, there was no other evidence of mammalian activity within the cave. Birds, reptiles and amphibians seemed to be completely absent.

Arthropods in the form of insects and arachnids were ubiquitous. A representative collection was made by Mr. Bridges and has been deposited in the American Museum of Natural History. They will form the basis of a separate report by Dr. W. J. Gertsch. Probably the most conspicuous insects were small flies which flew about our lights in large numbers. These flies were kindly identified by Dr. C. H. Curran, of the American Museum of Natural History, as *Phleomyia indecora* Lowe (Miliichiidae) and some *Psychoda* sp. (Psychodidae). The former was the predominant form. The most evident arachnids were large whip-scorpions which clung openly to the walls.

The bat guano contained great quantities of a macroscopic free-living nematode. When this material is finally studied it will probably be found to contain a fauna of some variety. This material is now in the hands of Dr. R. F. Nigrelli.

#### AQUATIC ORGANISMS.

The invertebrate aquatic organisms consisted of microscopic forms and two macroscopic forms. One, a crayfish, *Macrobrachium jamaicensis* (Herbst), which was lighter in color than those outside but with functional vision, is not to be considered as a cave form proper. Another, and smaller form, has been described as a new subspecies by Dr. H. H. Hobbs, Jr., under the name *Cambarus blandingii cuevachicae*, (Hobbs 1941). This lack of optical differentiation is equally true of the microfauna which is being studied by Dr. Nigrelli.

The only aquatic vertebrate encountered was the fish that the expedition set out to study. These fish had twice before been collected. Originally they were taken in 1936, as discussed in the introduction. Gordon and Coronado in 1939 made a hurried visit to the cave and took a second collection. In the first visit specimens were taken from Pools 1 and 2, while on the second they could be found only in Pool 2.

As neither party was equipped to go further than Pool 2, it remained for the present and third to examine the fish fauna to the workable end of the cave.

The most striking feature of this faunal unit was the discovery that these blind fish were not a uniform group. The fish previously collected were all blind and their offspring likewise grew up to be sightless creatures. Mr. Albert Greenberg of Tampa, Florida, has been especially successful in breeding this fish in captivity and obtained uniform material to the fifth generation. Shortly after the return of the expedition, a visit to his establishment showed that he had thousands of specimens of various ages, and he had noted that although he had reared them through five generations in light, all were completely blind.

It was quickly found in the cave that the fish ranged all the way from eyeless, pale creatures to fish that could not be distinguished from the normal river *Astyanax mexicanus* (Filippi).

The introduction of a light into the cave apparently causes those individuals endowed with eyes sufficiently perfect to recognize a light beam to retreat hastily, while the truly blind individuals seemed to give no attention to the strongest beam of a flashlight (See Breder & Gresser, 1941a, 1941b and 1941c). It was only after we had become thoroughly familiar with the cave and had baited the fish to given spots that we obtained the eyed and partially eyed forms.

Further, we found that there was a distinct gradient in that the further we went into the cave the more numerous became the fully eyed forms, and those fish not at all distinguishable from the normal river fish were only obtained beyond the large falls at Pool 3. Table II gives a measure of this gradient based on the arbitrary division of the fishes in blind, sunken eyed, covered and uncovered, and "normal-eyed," as based on our preserved collections. These rather arbitrary categories may be described as follows:

*Blind*—Eye socket covered with tissue level with the cheek, no evident eye structure.

*Sunken eye*—Some evident eye structure, but sunken below rim of orbit.

*Covered*—Evident sunken eye covered with tissue.

*Uncovered*—Evident sunken eye exposed as in a pit.

*"Normal"*—Eye convex and appearing as in a river fish, irrespective of its size, which was frequently very small.

Pigmentation followed a similar course although not fully correlated with eye structure. The pigmentation has been also arbitrarily divided, the five categories of which

TABLE II.  
Eye Condition and Pigmentation of Cave Characins.

Eye Condition					
Expressed in % of catch. Based on 119 specimens.					
Location <sup>1</sup>	Sunken Eye				"Normal" Eye
	Blind	Covered	Uncovered		
Sta. 1	85	6	—		9
Sta. 2	16 <sup>2</sup>	8	45		31
Sta. 3	—	9	9		82
Pigmentation					
Location	None	Little	Moderate	Considerable	Full
Sta. 1	90	2	6	2	—
Sta. 2	34 <sup>2</sup>	34	5	8	19
Sta. 3	3	29	32	24	12

<sup>1</sup> Sta. 1 indicates Pool II on map; Sta. 2, Pool III and Sta. 3, Pool IV.  
<sup>2</sup> Two specimens in this group blind on one side only.

are given in Table II. The extent of correlation of these two features associated with cave life are indicated in Table IV.

The sizes of the eyes of those fish with "normal" eyes are given in Table III, compared with river fish. Because of the variation in relative eye size with absolute size in fishes, this table has been broken into three size groups for purposes of comparison. From this treatment it is clear that the cave fishes extend from normal eye size to very small as compared with the river fish. Actually, the smaller eyed fishes taken in the river may represent a true genetic contaminant issuing from the cave or a general constitutional and initial eye variation in this group.

Since the connection with the river is from the far end of the cave there may be a more or less continual interchange between the river and cave fauna.

The cave ends, as far as human entry is concerned, in an elliptical chamber, the form of which is well indicated in the map and section together with the presumed underground exit of the flowing water. Here the Rio Tampaon is about half a mile distant.

A study of this variation in the eyes and pigmentation of these fishes must be reserved until an extended laboratory effort is made to obtain at least a basic understanding of the genetic foundation of this population. Because of the bearing on laboratory work the data of Tables II and IV have been used by Breder & Gresser (1941a).

During our visit to the cave, the fish were clearly in their reproductive season. Large females turgid with eggs were common as were small specimens that could not have been more than a month old. Mr. Greenberg found that in captivity the addition of some cold water to an aquarium would induce spawning, which led him to suppose that the rainy season might be the reproductive period. These two items taken together might be used to argue that spawning occurs throughout the year, the peak perhaps being reached when the rains come. Against this view would be the mechanical circumstances accompanying the torrential waters passing through the cave during that period, which would hardly seem friendly to spawning, especially of the type employed by these blind fish.

The sexes of the fish, together with their sizes, are given in Table V.

An attempt to examine the scales of these fish led to the surprising finding that replacement scales were the rule rather than the reverse. In fact, only thirteen of the twenty fish large enough to show markings were useful in this connection, as is indicated in Table V. Whether this is to be construed as evidence that due to swimming in the dark these fish continually knock scales off themselves or whether they take a serious battering when the torrents of the rainy season come, can only be speculated upon at this time. Although these fish under certain conditions will ram into objects, Breder & Gresser (1941a and 1941c),

TABLE III.  
Eye Size of Cave and Surface Characins.

Size Range S.L. in mm.	Expressed as % of standard length. Based on 69 specimens with "normal" measurable eyes.					
	Cave Specimens			Surface Specimens		
	Maximum	Mean	Minimum	Maximum	Mean	Minimum
0 - 30	11	9	7	12	11	10
31 - 60	10	7	5	10	8	6
61 - 90	8	6	5	8	8	8



TABLE IV.  
Association of Eye Condition and Extent of Pigmentation.

Eye Condition	Expressed in % of extent of pigmentation. Based on 119 specimens.				
	Extent of Pigmentation in Per Cent				
	None	Little	Moderate	Considerable	Full
Blind	98 <sup>1</sup>	—	2	—	—
Sunken Eye (covered)	56	33	11	—	—
Sunken Eye (uncovered)	—	62	15	15	8
"Normal"	2	23	28	23	24

<sup>1</sup> Two specimens in this group blind on one side only.

there is no observation noting that they dislodged scales by such accidents.

It would be unwarranted to attempt to define the nature of the markings on the scales as to whether they are annual or otherwise. While they seem to occur in a reasonable sequence with size, we have no way of equating this with time.

Although we know nothing of the various effects of their underground environment on the circulae of the scales, it must not be supposed that it is markedly uniform, for there is a clear annual cycle in the wet and dry season rhythm of this region. The fish are surely subjected to an annual change in temperature, quantity of water, rate of flow, food and perhaps in the chemical nature of the water itself.

The food problem, as already suggested by the presence of other than cave creatures, is simple in this cave. The great abundance of food objects leading directly to the outside renders the problem of primary diet quite simple. Organisms all the way from *Cyclops* and dipterous insects to the entire carcasses of bats are available to these fishes. Their stomach contents were found to consist of bat droppings and parts of other and smaller cave characins and their eggs. This would suggest that the only regular input of energy into the population for large parts of the year is bat dung. Their ability to thrive and reproduce on the ordinary foods supplied to small aquarium fishes also suggests the lack of any peculiar specialization in dietary requirements.

DISCUSSION.

The primary items of a cave fauna such as the present certainly center about the manner of establishment of a population of blind fishes and the nature of the association of lack of light and congenital blindness. Superficially simple-looking, critical examination of the possible development of such a condition presents some distinctly puzzling phases.

The finding of a long series of intermediates between the blind fish and the normal eyed river fish, which in itself is unique among cave fishes, gives hope that this material should prove of value in any attempt to understand this general association of blindness and darkness. Such a study, however, involves much further work.

As the situation stands, the facts in hand are subject to various interpretations. It might be assumed that these fishes in their normal river environment carry the genetic factors for an eye defect. Dr. C. L. Hubbs informs me that large series of Mexican *Astyanax* which he has examined show a surprisingly large amount of individual variation in eye diameter. Blind larval fishes

TABLE V.  
Size, Sex and Growth of Cave Characins.

Based on 119 specimens.															
Sex	Standard Length in mm.														
	Maximum		Mode						Minimum						
Female	83		45	50		40									
Male	62		50	55		38									
Immature	50		35	40		16									
Rings on Scales															
6													*	*	
5															
4										*		*	*		
3									*		*				
2									*	*		*			
1									*						
0	*	*	*	*	*	*	*	*	*	*					
	16	21	26	31	36	41	46	51	56	61	66	71	76	81	
	20	25	30	35	40	45	50	55	50	65	70	75	80	85	

Standard length in 5 mm. intervals.

Of the 20 fish above 55 mm. only 13 had other than replacement scales.

in the open river could hardly be expected to survive. However, with these fishes finding the way into cave waters, the eyed offspring presumably would have no advantage over the eyeless, resulting in the survival of some of each.

Following this thought along, two possible conditions suggest themselves.

It could be that such an entry was made some time ago and the resultant population as found is cut off from the river fauna and the eyed fish go on living in the absence of any detriment to having eyes, even if they cannot be used.

An alternative interpretation would be that there is a continual interchange of fishes between the cave and the river. It is not surprising that blind fish are not to be found in the river, for they clearly have strong disadvantages in such an environment, principally their blindness and conspicuous light hue. The contrary would not hold, and there may be a more or less continual penetration of the cave waters by normal river fish. If this latter view is correct, it would suggest that the development of such a population of blind fish took a much longer time than would the first alternative, because of the slowness of the spread of a character that is evidently recessive in a continually diluting population.

The finding of a progressive series of eyed fishes as one moves toward the river encourages such a view.

A quite different interpretation would be to assume that at some distant time a group of fish became entrained in this cave in a state of complete isolation and became blind by whatever mechanism operates under such conditions. Then a further assumption would be made that this population of thoroughly blind fish again came in contact with the normal river fish from which they were originally derived. The resultant stock as found would then be the hybrid mixture of these two groups. The increasingly higher number of eyed fishes as one nears the river would be compatible with this view.

Other views concerning the possible direct effect of environment on vision and pigmentation find little support in the present material. There are eyed and intermediates living in the cave successfully with the eyeless for an unknown number of generations. Five generations of the entirely blind stock reared in brilliant light show no suggestion of returning vision or pigmentation.

Experimental studies are here called for and in the words of Gresser & Breder (1940), "Until at least some of these are undertaken, it would seem to be pointless to attempt further speculation." Progress in this direction has already been made and is reported in Breder & Gresser (1941a, 1941b and 1941c).

#### SUMMARY.

1. La Cueva Chica is able to support a population of temperature limited characins by virtue of nearby thermal waters which prevent the subterranean waters from falling below a relatively high value.

2. The cave characins are supported by a large variety of food items which trace directly or indirectly to the outside by way of bat droppings.

3. The cave characins (*Anoptichthys jordani*) show complete intergradation with the river characins (*Astyanax mexicanus*) through a long series of individuals with intermediate eyes and pigmentation and surely represent a single population. There is a pronounced gradient in these features from one end of the cave to the other.

4. Other animal organisms found living in the cave, bats, crustaceans, insects, spiders and related forms and a considerable microfauna, are not modified in any way comparable to that of the fishes and are not confined exclusively to a cave habitat.

5. The cave itself, small in extent, so far as human entry is concerned, except for its high temperature is typical of limestone formations and shows no other exceptional features.

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EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1.

Calcareous scum on the surface of Pool No. 1. Photo by E. B. Gresser.
- Fig. 2.

Blind fish as found in Pool No. 2. Here the individuals are nearly all of the fully blind type. This is the place from which the original collection was made, representing at once the exact type locality as well as the source of the parent stock of this form now to be obtained from dealers. Photo by S. C. Dunton.
- Fig. 3.

Cup-like basins below Pool No. 2. Photo by S. C. Dunton.

PLATE II.

- Fig. 4.

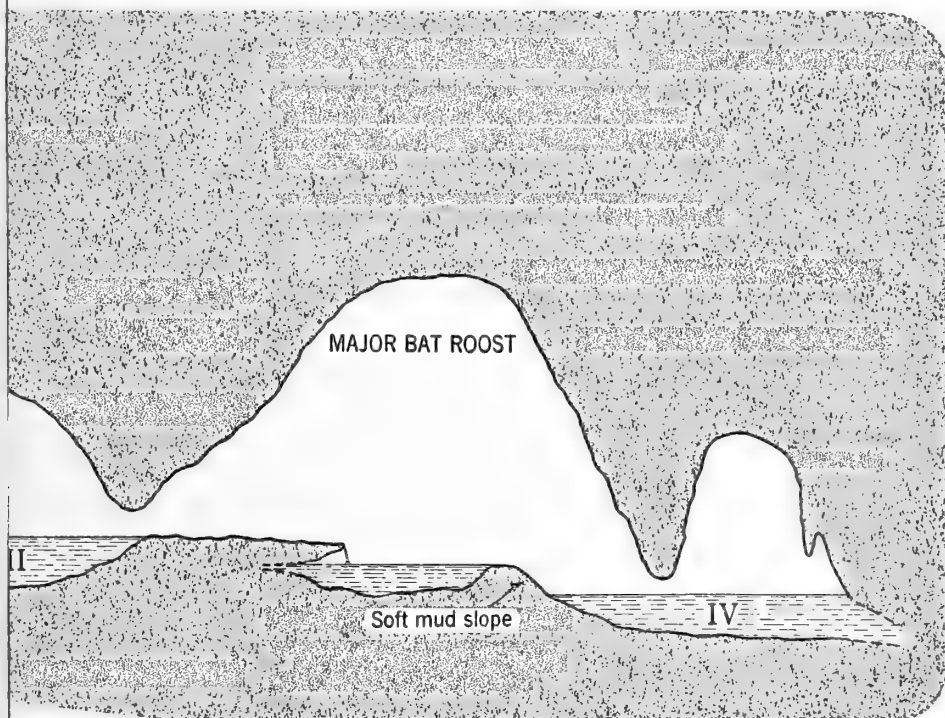
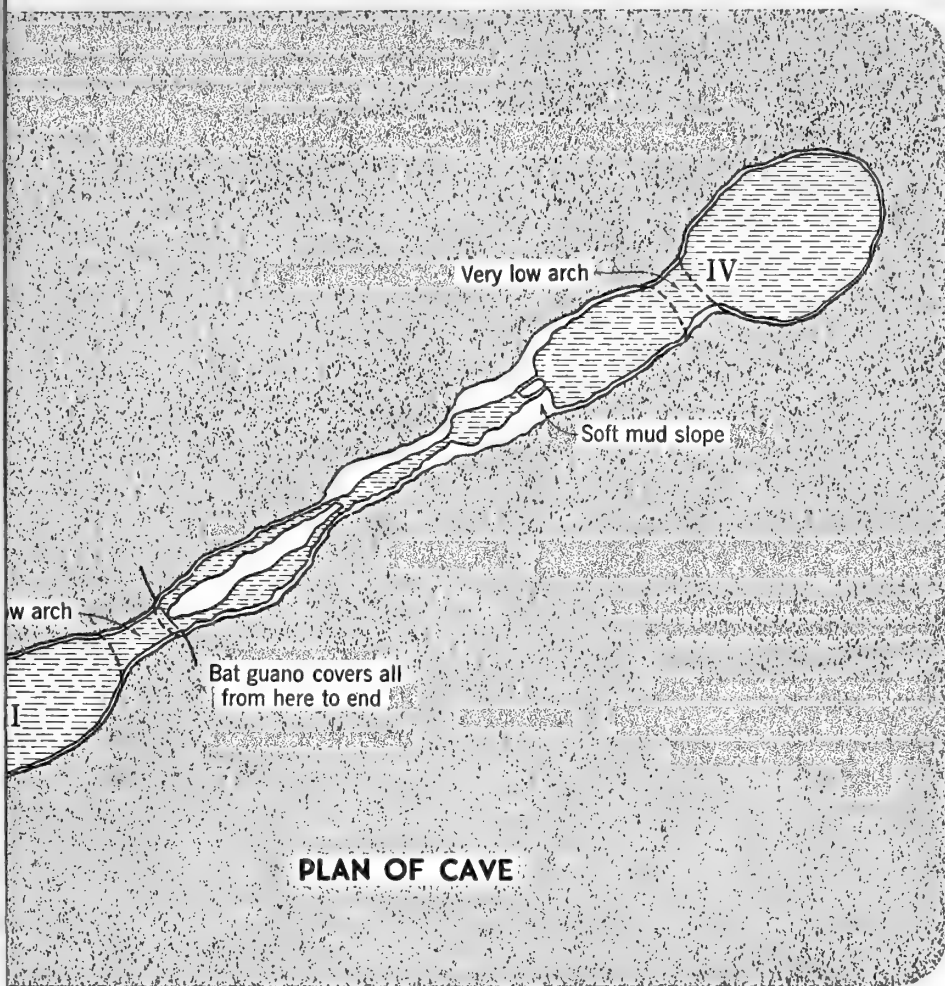
Pool No. 4, showing the low arch across its middle. The material floating on the water is caked bat guano. Photo by S. C. Dunton.

PLATE III.

- Fig. 5.

Cave fish in various stages of eye degeneration. Reading from the top down: Fully blind and pigmentless type; Somewhat pigmented with a miniature eye; "normal" fish from cave; "normal" fish from the Rio Tapaon. Photo by S. C. Dunton.













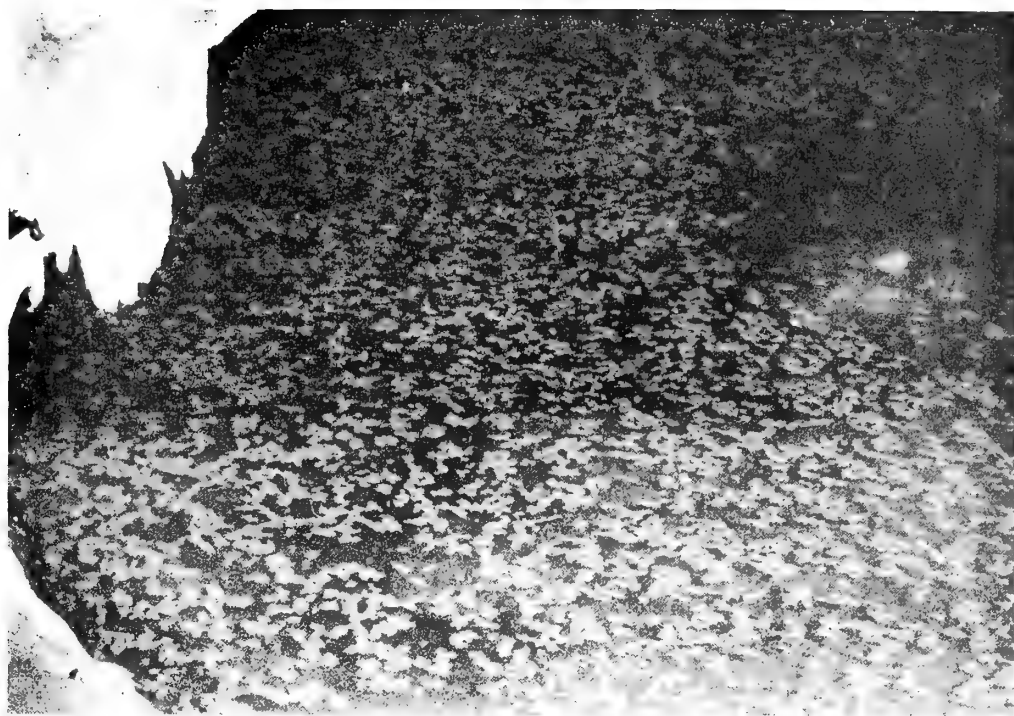


FIG. 1.

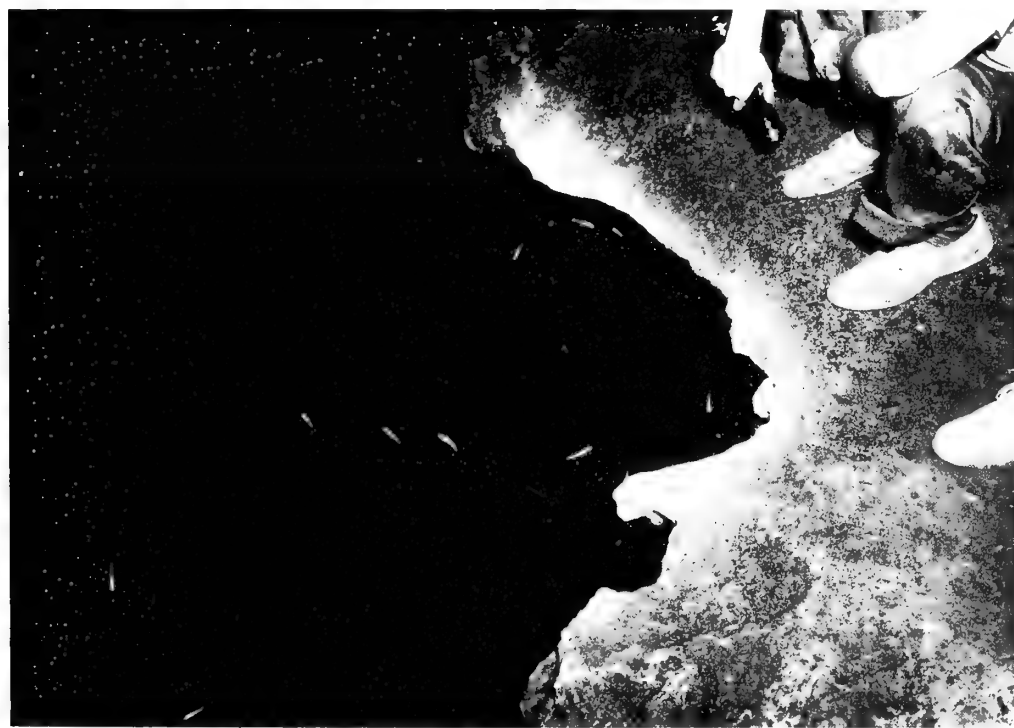


FIG. 2.

DESCRIPTIVE ECOLOGY OF LA CUEVA CHICA, WITH ESPECIAL REFERENCE  
TO THE BLIND FISH, *ANOPTICHTHYS*.

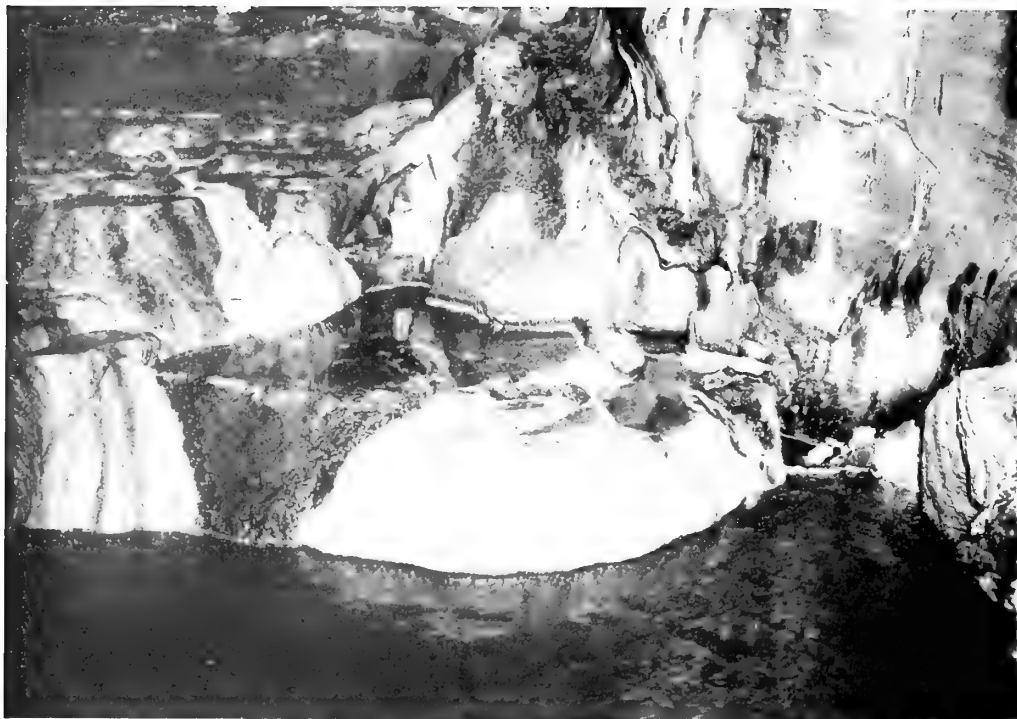


FIG. 3.



FIG. 4.

DESCRIPTIVE ECOLOGY OF LA CUEVA CHICA, WITH ESPECIAL REFERENCE  
TO THE BLIND FISH, *ANOPTICHTHYS*.

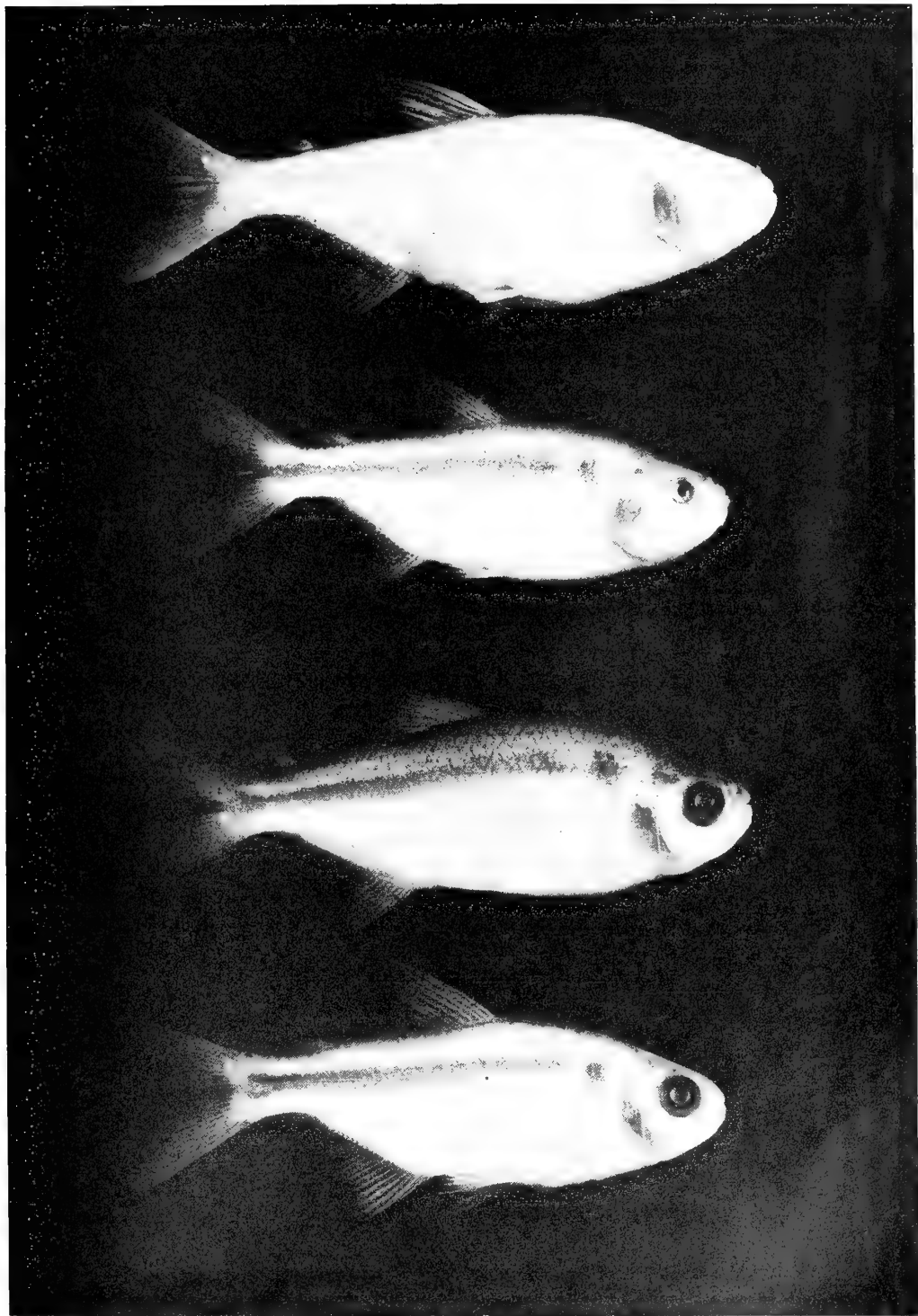


FIG. 5.

DESCRIPTIVE ECOLOGY OF LA CUEVA CHICA, WITH ESPECIAL REFERENCE  
TO THE BLIND FISH, *ANOPTICHTHYS*.



## 4.

## Quantitative Serologic Relationships Within the Artiodactyla.<sup>1</sup>

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(Text-figure 1).

### INTRODUCTION.

Any study of animal relationships justifies the use of a serological method capable of stating in exact mathematical terms the degree of relationship of the animals being studied. In the present study a volumetric quantitative precipitin technique having these qualifications was employed in a study of the blood sera of some Bovidae and Cervidae.

Although the precipitin reaction has been used in the study of plant and animal relationships since 1900, only a few investigators have thought of its use in exact quantitative terms. Boyden (1926) expressed its quantitative nature and stated that measurements of degree of relationship so obtained are independent of interpretation. Further elaborating on the idea, Boyden & Baier (1929) devised an exact quantitative volumetric precipitin technique that is "simpler and more rapid than any other which has been used in the quantitative study of blood relationships, and that through it highly significant *measurements* of biological relationships may be made." Their technique of measuring volumetrically the amount of precipitate formed in the reaction was a decided improvement over the methods of Nuttall (1904), Schur (1904), Hamburger (1905), and Mollison (1924), in that of all these workers, they were the only ones who gave an adequate statement of the reliability of their technique. In one series of 36 determinations the average error of the individual readings was 5 per cent. when compared with the mean of the series. The average deviation of the means of successive pairs of readings was the same as the deviation of the whole series, while the means

of the values taken in quartets dropped to 3 per cent. An error in technique of this value, when supported by statistical analysis, is indeed very significant. According to Boyden (1934), "the results of the application of such a technique to the study of serologic relationships should be of great interest. It is likely that this technique will succeed in distinguishing closely related species, which have heretofore been indistinguishable by the precipitin test." So far, this is the only volumetric test which has been used in serological relationships.

Using this improved volumetric technique, Baier (1933) established the constancy of in-vitro factors for proper execution of the tests. Wolfe & Baier (1938) by using the ring test and the volumetric precipitate measurement procedure showed that the in vivo injection procedure may influence the "type" of precipitin that may be produced. They found that high-titered (ring test) antisera were produced by one or two series of injections of undiluted antigen while continued re-injections resulted in an increase in the precipitate forming power of an antiserum without causing an increase in the ring test "titer" of the antiserum. They indicated the presence of (1) a "titer"-producing antibody and (2) a "precipitate"-forming antibody. It is important when attempting volumetric relationship studies that an antiserum be employed having high precipitate forming powers.

A more recent technique of precipitate measurement which should parallel the volumetric technique is that of the Libby Photorefractometer (Libby, 1938) which measures the amount of precipitate formed in the precipitin reaction by nephelometric methods. So far two papers have appeared (Boyden, 1938, and DeFalco, 1941) indicating its possible use in relationship studies.

With the reliability of the volumetric technique well established, an investigation

<sup>1</sup>The Works Progress Administration furnished personnel assistance under the University Natural Science Project, Work Project No. 10324 for this research.

The authors wish to thank the various contributors listed in Table I for furnishing the samples of blood sera used in this study.

of the serological relationships of some Bovidae and Cervidae was attempted to parallel a similar study of Wolfe (1939) who reported on some of these same samples of blood. In his paper, however, only the "ring" test was employed.

The earliest work of actual precipitate measurement in a problem of animal relationship studies is that of Nuttall (1904), who with Strangeways reported, among others, some studies made with the bloods of some Cervidae and Bovidae. Since then only the paper of Boyden (1934) reported one brief study of an ox-sheep reaction as a suggestion of the possible use of a volumetric precipitin technique.

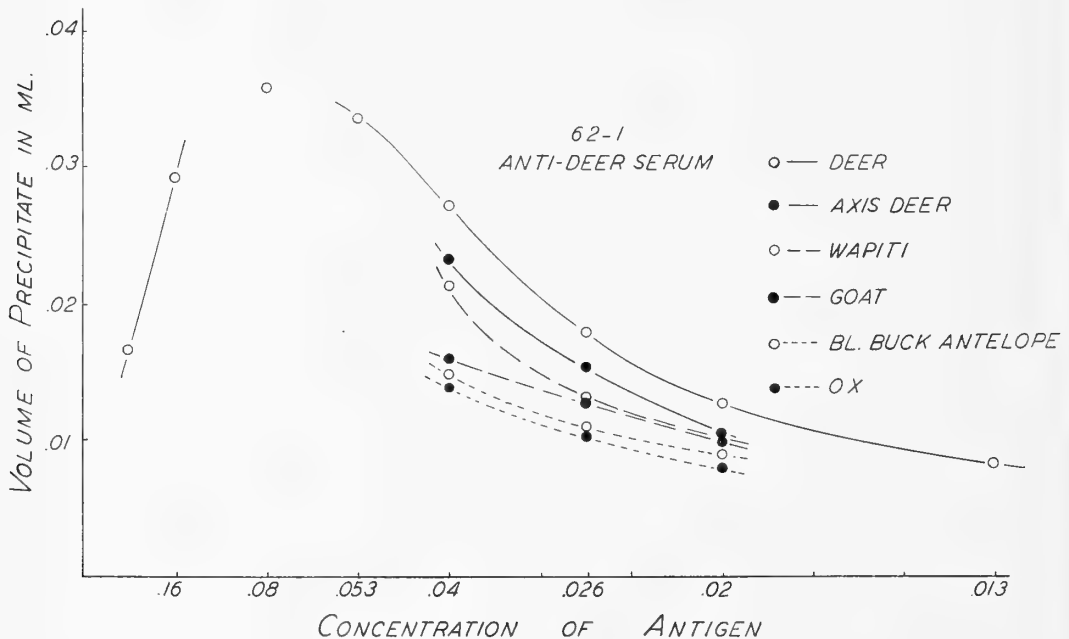
#### MATERIALS AND METHODS

Antibodies were produced in healthy adult male and female rabbits of various breeds. The undiluted serum antigens were injected intravenously at intervals of a month or more; the initial series of injections consisted of three injections given on alternate days and the total quantity of antigen injected was 3 ml. Subsequent series of injections consisted of two injections on alternate days of a total of 1.5 ml. This method of antigen injection was shown by the authors (1938) to be conducive to the production of good precipitating antisera.

The animals were bled from the heart with sterile syringes and needles, the blood allowed to clot, and the exuded serum filtered through Seitz filters. The serum was transferred to sterile ampoules and stored in the refrigerator until used.

The serum antigens used for antibody production (Table I) were deer, ox, buffalo, sheep, and goat. Test antigens consisted of various species of Artiodactyla (Table II).

The tests, in vitro, were carried out following the method of Boyden & Baier (1929) using standardized Van Allen thrombocytocrits to measure volumetrically the precipitate obtained by incubating known amounts of antigen and antiserum. Mixtures of 0.5 ml. of antiserum and 0.5 ml. of antigen (either homologous or heterologous), diluted to give a protein content so as to stay in the range of relative antibody excess, were made directly into the thrombocytocrits. These were then placed in a water bath at  $37.5^{\circ} \pm 0.5^{\circ} \text{C}$  for one hour and centrifuged for two fifteen-minute periods in a tachometer controlled centrifuge at the rate of 2,400 R.P.M. Readings were made in duplicate and sometimes in quadruplicate. The protein content of all antigens was based on total nitrogen which was determined by a modified macro-Kjeldahl method. The test antigens were standardized to give similar protein content by diluting with buffered saline (Evans, 1922). It was necessary at times to dilute the antiserum with buffered saline in order to avoid an excessive amount of precipitate. Tests with any one antiserum were always made at a constant dilution of antiserum. Any variations in the measurable precipitate were due then to differences in the proteins of the various blood sera used in these relationship studies. Relationships were recorded in terms of the percentage of volume given by a heterolog-



ous determination in comparison to the homologous precipitate volume taken as 100 per cent. The average of at least six readings on the curve of reaction, of three different antigen concentrations in the area of relative antibody excess was taken for any one relationship value. By using six readings as a minimum the statistical reliability of the test could be established (Boyden & Baier, 1929) and by taking these readings from the area of relative antibody excess the resolution of the precipitate by excess antigen could be avoided as well as obtaining a greater constancy in the readings (Baier, 1933). He also demonstrated that it is not advisable to use the entire curve of reaction since readings taken in the area of antigen-antibody equilibrium are unreliable. Text-fig. 1, taken at random from Table V, illustrates these points from the reaction of anti-deer serum with the homologous and heterologous antigens used in this study. The region of relative antigen-antibody equilibrium is shown as the discontinuous peak of the curve. To the left is the area of antigen excess, while to the right is shown the area of antibody excess where the

heterologous readings were made for relationship studies.

### RESULTS.

In Table III are presented the data obtained from two anti-ox and one anti-buffalo sera. These antisera were reacted with their homologous antigens and with several heterologous antigens.

The data of 21-3 and 22-2 show that the buffalo and eland sera are more closely related to ox than are the sera of the other Bovidae or the Cervidae. Furthermore, the per cent. values indicate that buffalo is more closely related to ox than is the eland. This essentially verifies the results of Wolfe (1939), but it should be emphasized that the technique employed in the present paper enables a distinction between ox and buffalo antigens which he could not show using the ring test with unabsorbed sera.

The two ox antisera did not give similar degrees of reaction in per cent. with the heterologous antigens but the relative positions of the animals was constant. Similar results will be noted throughout this paper. It is advisable, therefore, to emphasize

TABLE I.  
Test antigens.

Family	Scientific Name	Common Name	Source of Material
Bovidae	<i>Bos taurus</i>	Ox (2 samples)	Mayer Packing Company
	<i>Bison bison</i>	American buffalo	Yellowstone National Park
	<i>Taurotragus oryx</i>	Eland	New York Zoo
	<i>Poëphagus grunniens</i>	Yak	San Diego Zoo
	<i>Anoa depressicornis</i>	Anoa	New York Zoo
	<i>Ovis aries</i>	Sheep (3 samples)	Mayer Packing Company
	<i>Capra hircus</i>	Goat	University Farm
	<i>Ovis tragelaphus</i>	Aoudad	New York Zoo
	<i>Ovis canadensis</i> by <i>Ovis musimon</i>	Mountain sheep hybrid	San Diego Zoo
	<i>Antelope cervicapra</i>	Black buck antelope	New York Zoo
Cervidae	<i>Odocoileus virginianus</i>	White-tailed or Virginia deer	Madison Zoo
	<i>Cervus axis</i>	Axis deer	New York Zoo
	<i>Cervus canadensis</i>	Wapiti (2 samples)	New York Zoo

TABLE II.

Rabbit Number	Antigen Injected	Series of Injections	Quantity Injected		Bled (days following last injection)	Homologous Titer (ring-test)
			First Series (undiluted)	Additional Series (undiluted)		
21-3	Ox	4	3 ml.	1.5 ml.	10	1,024,000
22-2	Ox	3	3 ml.	1.5 ml.	10	256,000
54-2	Buffalo	3	3 ml.	1.5 ml.	10	512,000
30-2	Sheep	3	3 ml.	1.5 ml.	10	512,000
50-3	Goat	4	*	1.5 ml.	10	512,000
51-3	Goat	4	*	1.5 ml.	10	256,000
62-1	Virginia deer	2	*	1.5 ml.	7	512,000
62-2	Virginia deer	3		1.5 ml.	7	512,000
62-3	Virginia deer	4		1.5 ml.	8	512,000
62-4	Virginia deer	5		1.5 ml.	8	512,000
62-5	Virginia deer	6		1.5 ml.	8	512,000

\* Between .75 to 1.5 mg. total protein per kg. of body weight. This is actually the second series of injections as the animals were previously injected with minute quantities and reported by Wolfe (1939).

TABLE III.

Antigen	21-3 anti-beef	Antisera anti-beef 22-2	anti-buffalo 54-2
Ox - 1	100.0	100.0	78.8
Buffalo	94.3	84.9	100.0
Eland	84.8	64.17	—
Yak	—	—	77.7
Anoa	—	—	74.4
Sheep - 5	44.9	52.90	—
Sheep - 6	—	54.53	—
Sheep - 6W	—	—	38.4
Goat	36.0	53.03	—
*Black buck antelope	42.2	32.47	22.7
*Wapiti	43.71	42.8	30.7
*Axis deer	50.13	39.23	42.3
Virginia deer	45.8	53.93	44.8

\*Data may not be reliable due to excessive hemoglobin in test samples.

phylogenetic position rather than actual percent. relationship.

The percentages in the reactions of the Bovidae sera, other than the buffalo and eland, and of the Cervidae sera, were, on the whole, quite similar. Thus the wapiti, Virginia deer and axis deer seem to be as closely related to the ox as are the sheep, goat and black buck antelope. Since such closely related forms as the goat and sheep or the axis deer and wapiti did not, as would be expected, give similar percentage reactions, it seems necessary to treat the more distantly related forms as a group, rather than to attempt to give each animal a definite position in the table.

The buffalo antiserum (54-2) was reacted with yak and anoa bloods as well as with some of the antigens tested with ox antisera. The ox, yak, and anoa bloods all gave similar percentages and showed a much closer relationship to buffalo than did the other Bovidae and Cervidae. This result was to be expected. Again the more distantly related forms gave inconsistent results and must be treated as a group.

Table IV presents the data obtained from

anti-sheep and anti-goat sera reacted against their homologous antigens as well as representative heterologous antigens. The anti-sheep serum (30-2) was able to distinguish between sheep and goat sera, and their high percentage values indicate a closeness in the relationships of these forms. That these percentage values are statistically reliable is indicated by the ratios of the means to their respective probable errors. For sheep-6 serum the ratio was 55:1, while for goat serum the ratio of the mean to the probable error of the mean was 140:1. These figures, in being well above the 4:1 ratio generally accepted as indicating statistical reliability, are highly reliable in stating that by means of this volumetric test it was possible to distinguish sheep serum from goat serum which had not been hitherto usually possible using the ring test with unabsorbed sera. The order of relationship for the other animals indicated that ox and buffalo were more closely related to the sheep than were the Virginia deer, black buck antelope, eland, axis deer and wapiti. The reactions of the sera of these distantly related forms did not give the consistent re-

TABLE IV.

Antigens	30-2 anti-sheep	Antisera 50-3 anti-goat	51-3 anti-goat
Sheep - 6	100.0	—	—
Sheep - 5	99.60	91.9	63.8
Goat	96.30	100.0	100.0
Aoudad	—	84.3	—
Mountain sheep hybrid	—	81.2	—
Ox - 1	87.40	42.8	27.6
Buffalo	85.57	44.7	24.8
Eland	70.40	—	—
*Black buck antelope	71.57	—	—
Virginia deer	77.27	51.3	30.7
*Axis deer	68.53	40.9	20.5
*Wapiti - 1	61.7	—	23.1
*Wapiti - 2	—	54.8	22.8

\*Data may not be reliable due to excessive hemoglobin in test antigens.



sults expected of closely related forms and these species should be regarded as a group rather than individually.

The two anti-goat sera (50-3, 51-3) were more specific than the anti-sheep serum. The sheep serum again could be distinguished from the goat serum, and the high percentage reaction of the aoudad and mountain sheep hybrid show their closeness to the goat. On the other hand, the remaining Bovidae and Cervidae reactions were lower and it cannot be said which ones are more closely related to the goat. This result is consistent with the data for anti-ox and anti-buffalo sera presented in Table III.

Antigoat serum 51-3 gave much lower percentages with the heterologous antigens than did 50-3, indicating that the former serum can be considered to be more specific. Such differences in serum specificity are also known to occur with the ring test method.

Table V illustrates the data of five anti-Virginia deer sera produced in a single rabbit. This rabbit was given several series of injections and bled after each series. Animals injected by this method were shown by Wolfe & Baier (1938) to produce high precipitating antisera useful in quantitative volumetric precipitin studies but giving very aspecific reactions if the ring test technique is used.

The reactions of all five antisera gave larger amounts of precipitate with members of the deer family than with the Bovidae. In every case the axis deer and wapiti could be distinguished readily from the Virginia deer, while the Bovidae gave considerably lower percentage values. The relative closeness of the axis deer and wapiti to the Virginia deer is not definite from the data presented. In two out of three instances where both tests were made the axis deer showed the closer relationship, but in the other just the opposite condition was observed. Then again, the two wapiti bloods do not give the same degree of reaction. The only explanation the authors wish to offer is that these

samples of sera contained a large amount of hemoglobin and possibly the per cent. of protein, obtained on the basis of total nitrogen, was inaccurate. The authors feel that exact protein content of the active antigens is essential and disagreements of the type illustrated can be avoided only if better methods can be devised for measuring only the reactable antigens.

DISCUSSION.

The data presented in this paper confirm and extend the evidences for facts concerning the blood relationships of some species of Bovidae and Cervidae previously shown by morphological and by other serological techniques.

That morphology has its place in phylogeny is not disputed; that it has its limitations is evident. The serologist can apply his studies to a more exact and quantitative estimation of present relationships with a technique which is independent of morphology. This is the aim of the present paper.

The volumetric method of measuring the amount of precipitate formed in the precipitin test has enabled a distinction between some very closely related forms. Thus ox and buffalo, and sheep and goat could be distinguished from each other. This is usually not possible with unabsorbed antisera using the ring test. The advantages of the volumetric test over the ring test is of this nature. Its disadvantages are that the test is time-consuming in its operation, protein contents of all test antigens must be very accurately determined, and as to the data, it has not been possible so far to indicate the degree of relationship of more distantly related forms. It is hard to explain why the more distantly related forms reported in this paper show inconsistent degrees of relationship to a test antiserum and why all of these distantly related forms, regardless of their phylogenetic position, show about the same per cent. of distant relationship. No attempt was made to study

TABLE V.

Antigen	Anti-Virginia Deer Sera				
	62-1	62-2	62-3	62-4	62-5
Virginia deer	100.0	100.0	100.0	100.0	100.0
*Axis deer	83.7	—	96.4	72.4	59.6
*Wapiti - 1	76.2	66.3	88.6	—	66.4
*Wapiti - 2	—	77.0	—	—	78.1
Goat	69.1	43.7	76.8	56.8	—
Sheep - 5	—	45.9	77.2	69.6	50.6
Ox - 1	—	44.7	70.9	—	48.8
Ox - 5	57.1	—	—	—	—
Buffalo	—	41.6	76.8	63.5	53.2
Eland	—	40.6	—	50.9	—
*Black buck antelope	60.9	37.3	61.9	59.0	—

\* Data may not be reliable due to excessive hemoglobin in the test antigens.

this problem at the present time; distantly related forms were merely spoken of as a group rather than as individuals.

A possible explanation may be that the relative position of the region of antibody-antigen equilibrium in shifting toward the left (refer to Text-fig. 1), as reactable antigen decreases and toward the right as reactable antigen increases will alter the nature of the curves being studied, and only by studying antigens having approximately the same reactable antigen content will the curves of reaction be reliable. No degree of controlling total antigen content by means of Kjeldahl determinations can alleviate this difficulty as the Kjeldahl determinations measure the total protein content of test antigens and not the per cent. of reactable or specific protein antigens.

The ring test titers on the other hand, are not influenced either by slight variations in protein concentration or by the proportions of antigen and antibody in the reaction mixtures since the end point used (titer) is simply the maximum dilution of an antigen that will form a ring of precipitate at the junction of antigen and antibody.

Comparisons of the data obtained by the ring test and by the present volumetric technique can be made by referring to the paper of Wolfe (1939), who reported on three of the rabbits used to produce antisera in the present paper. These rabbits (numbers 50, 51, and 62) were given one series of minute injections of antigen to produce the specific antisera required to distinguish closely related forms using the ring test, and were then given additional series of larger injections to produce the high precipitate forming antisera for use in the volumetric precipitin test. The results are in general agreement as has been stated previously.

The technique employed has consistently enabled a distinction of such closely related forms as ox from buffalo, sheep from goat, and Virginia deer from axis deer and wapiti. Were the ring test to be employed, such distinctions could not be consistently made with undiluted sera. The volumetric method used in this paper seems to be a very reliable one in showing the differences of very closely related forms. On the other hand, the more distantly related forms used in this work can be classified together only as a group rather than as individuals. A more or less rough grouping is possible from the data presented. The more closely related forms could be placed in one group and subdivided according to their closeness of relationship while the more distantly related forms were placed in a second group and subdivision was not possible except in one instance (anti-sheep serum).

In tabular form, this data can be pre-

sented as a brief serological classification in the following fashion.

- A. Classification based on anti-beef sera
  - Group I
    - A. Ox
    - B. Buffalo
    - C. Eland
  - Group II
    - Other Bovidae and Cervidae tested
- B. Classification based on anti-buffalo serum
  - Group I
    - A. Buffalo
    - B. Ox, yak, anoa
  - Group II
    - Other Bovidae and Cervidae
- C. Classification based on anti-sheep serum
  - Group I
    - A. Sheep
    - B. Goat
  - Group II
    - A. Ox, buffalo
    - B. Other Bovidae and Cervidae
- D. Classification based on anti-goat sera
  - Group I
    - A. Goat
    - B. Sheep
    - C. Aoudad, mountain sheep hybrid
  - Group II
    - Other Bovidae and Cervidae
- E. Classification based on anti-deer sera
  - Group I
    - A. Virginia deer
    - B. Axis deer and wapiti
  - Group II
    - Bovidae

#### SUMMARY.

1. The sera of thirteen representative species of Bovidae and Cervidae were used as test antigens.
2. Eleven antisera were produced against five of these thirteen species.
3. Antisera were produced having high precipitate forming powers.
4. The per cent. of relationship is reported on the basis of the volume of precipitate formed in the reaction mixture when compared with the homologous reaction taken as 100%.
5. Ox, buffalo and eland are related to each other in the order named, and could be distinguished from each other.
6. Virginia deer could be distinguished from axis deer and wapiti.
7. Ox, yak and anoa are closely related to buffalo.
8. Sheep and goat could be distinguished from each other.
9. Aoudad and mountain sheep hybrid could be distinguished from goat and these forms were more closely related than were the other Bovidae.
10. This work confirms ring test studies, but enables a finer distinction of closely related forms.

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## 5.

**Observations on the Electric Discharge of  
*Torpedo occidentalis*.**

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(Text-figures 1-4).

In June of 1941 a specimen of *Torpedo occidentalis* was brought to the New York Aquarium and several more were brought in during the next few weeks. These were all large, in excess of 15 kilograms in weight, and one was very large, 61 kilograms, probably a record size.

A few electrical measurements were made on the first of these fish within a few hours after its arrival at the Aquarium. Circumstances unfortunately delayed further observations, and before they could be resumed all these specimens died. Two others, however, remained available at Point Lookout, Long Island, at the fish pier of Mr. Robert Doxsee, from whom the former specimens had been obtained. To avoid possible injury to these fish by the handling necessary in transporting them, it was thought advisable to observe them without bringing them to the Aquarium. Through the courtesy of Mr. Doxsee a cathode-ray oscillograph and accessory equipment were set up at Point Lookout, partly on the pier and partly on the live well floating alongside, in which the fish were kept. Observations under these conditions were somewhat difficult and, what was more unfortunate, the two fish, after having been for several weeks in the live well, were evidently in very poor condition.

Although for these reasons our observations are necessarily rather fragmentary, they appear to contain some information not recorded elsewhere, and a brief report on them would thus seem to be worth while.

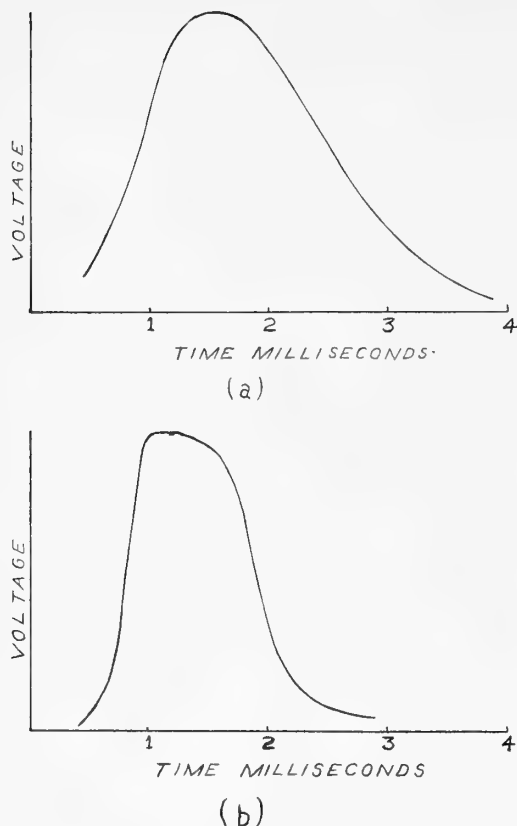
The first specimen showed a peak voltage of 220 volts when the dorsal and ventral surfaces of its electric organ on one side were connected to the oscillograph on "open circuit," so that no appreciable current was

drawn except what flowed in the circuit made through the body of the fish. Except for the voltage drop caused by this current, the full electromotive force would have been measured in this way. Probably the electromotive force was not much higher than the measured peak voltage, and may therefore be taken as approximately 220 volts.

In this species, however, the electromotive force appears to vary widely with the condition of the fish. The measurements made on this specimen were so arranged as to keep the fish out of water as short a time as possible. Actually they were all completed in about one minute. We can not say how many discharges were made in this time; there were certainly several hundred, possibly a thousand. Whether from being out of water, from fatigue, or from the handling incidental to the measurements, the peak voltage on open circuit dropped 60 volts during this time. More striking still was the difference between this specimen and the two observed at Point Lookout. Although these were of about the same size as the first specimen, their peak voltage on open circuit was only about 25 volts.

The oscillographic traces produced by the first specimen were not recorded photographically but only noted visually. Even so, certain differences between the traces made by the torpedo and those made by the electric eel and described elsewhere<sup>1</sup> were evident. The discharge of the torpedo did not show so sudden a rise in voltage or so abrupt a transition from a rapidly rising to a gently falling voltage. A few photographic

<sup>1</sup> Coates, C. W., R. T. Cox, and L. P. Granath. The Electric Discharge of the Electric Eel, *Electrophorus electricus* (Linnaeus). *Zoologica*, Vol. XXII (Part 1), No. 1, April 5, 1937.



Text-fig. 1. **a.** Oscillographic trace of the electric discharge of *Torpedo occidentalis*. **b.** Oscillographic trace of the discharge of *Electrophorus electricus*.

traces were obtained of the discharge of one of the two specimens observed at Point Lookout. Text-fig. 1(a) was drawn from one of these: 1(b), shown for comparison, was made from a photographic trace produced by the electric eel. In copying from the photographs, the time scale was made the same for the two figures. The scales of voltage are different between the two, having been so chosen as to make both peaks of the same height. It is apparent that the duration of the discharge of the torpedo was longer than that of the discharge of the electric eel. But it should be repeated that the discharge shown for *Torpedo* is that of a specimen in poor condition.

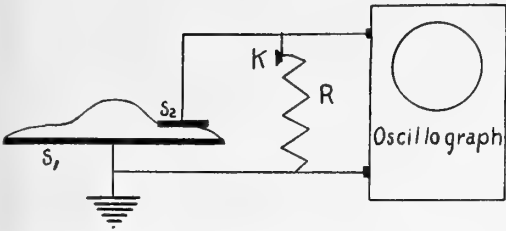
The electric organs of *Torpedo occidentalis*, like the large organs of the electric eel, throw off discharges in trains, the separate discharges following one another at an interval of a millisecond or so. With the specimen first observed there were more discharges in one train than the three, four, or five commonly observed with the electric eel. Without a photographic record, it can not be said just how many there were. Prob-

ably there were at least a dozen in the average train. The photographic traces obtained at Point Lookout, perhaps because of the poor condition of the specimen, showed fewer discharges to the train than were observed with the first specimen.

The observed regularity of the discharges within a train and in successive trains suggested that the same quantity of tissue was active in each discharge, and it is natural to suppose that the entire organ connected to the oscillograph was active together. Also it was possible to show plainly that the right and left organs discharged simultaneously. The method used was that employed before to measure the time lag between the discharge in anterior and posterior portions of the large organs of the electric eel, and it had been described elsewhere.<sup>2</sup> One of the vertically deflecting plates in the oscillograph tube being joined to one of the horizontally deflecting plates, their junction was connected to a large sheet of metal on which the torpedo rested, the ventral surfaces of both organs being over the plate. Two smaller sheets, some distance apart on the dorsal surface of the fish, covered the two organs on that surface. These two sheets were connected respectively to the other two deflecting plates of the oscillograph tube, so that the discharge of the organ on one side would produce a vertical deflection and that on the other side a horizontal deflection. (Strictly speaking, the discharge on one side would produce a nearly vertical, that on the other a nearly horizontal, deflection, the complete separation of the two deflections being prevented by leakage of the current across the body of the fish from one side to the other. An auxiliary observation, in which one sheet was over the organ on one side while the other was over non-electric tissue, was used to estimate the possible effect of this leakage). Both organs discharging exactly together would produce equal vertical and horizontal deflections, and thus would combine to make an oscillographic trace along a straight line at 45 degrees with either the vertical or the horizontal direction. A small time lag between the discharges of the two organs would change the trace into a loop, the width of the loop being greater the greater the time lag. Actually the trace appeared simply as a straight line. Had there been a time lag as great as .0001 sec. it should have been detectible by this method.

Some muscular activity accompanies the discharge of *Torpedo occidentalis*. The fish, which is flat and roughly disk-like in shape, showed distinct tremors around the periph-

<sup>2</sup> Coates, C. W., R. T. Cox, W. A. Rosenblith, and M. Vertner Brown. Propagation of the Electric Impulse Along the Organs of the Electric Eel, *Electrophorus electricus* (Linnaeus), *Zoologica*, Vol. XXV (Part 2), No. 14, July 3, 1940.



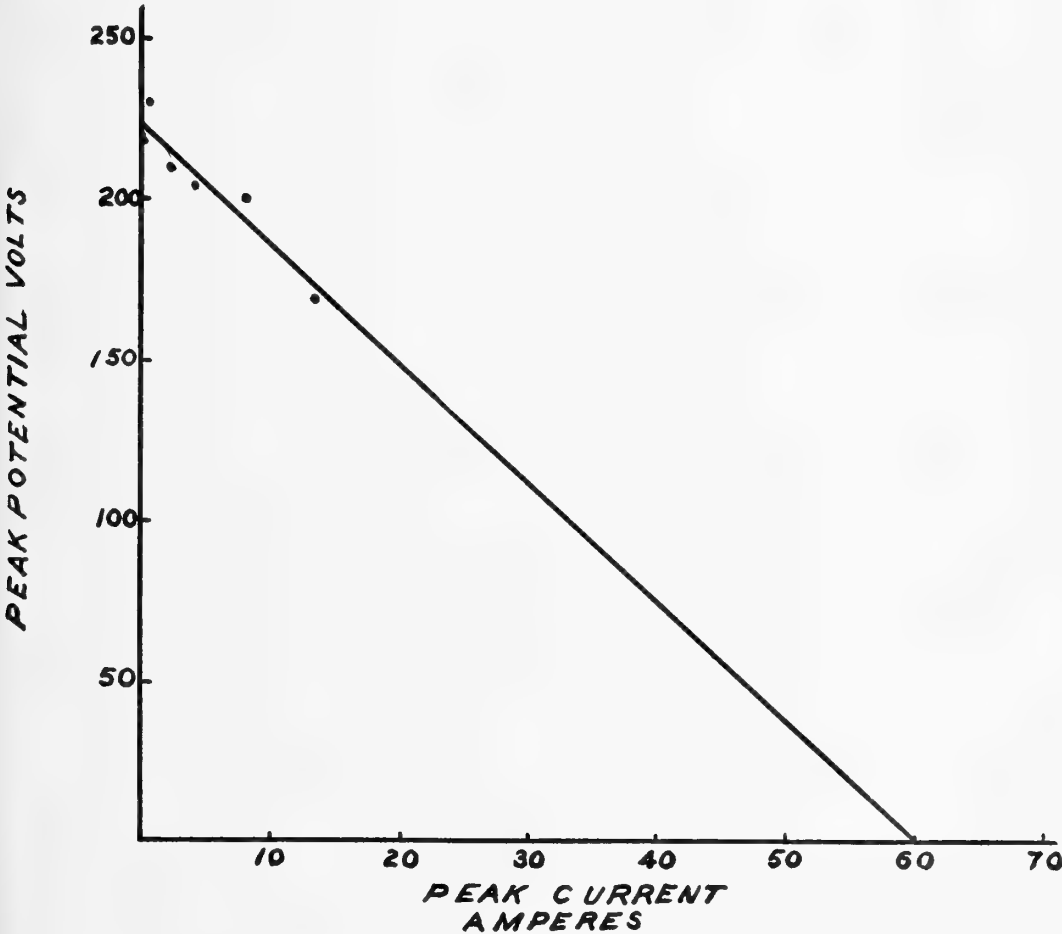
Text-fig. 2. Diagram of the electric circuit for the measurement of the peak voltage of the discharge.

ery of the body when the discharge occurred, although it is not certain whether these were directly before or during the train of discharges. This activity caused the margins of the wings to curl upward, sometimes more than 10 cm. from the surface on which the fish was lying. During a long series of discharges these margins were raised throughout the period with accompanying tremors starting from the thick central

region of the body and spreading outward to the periphery.

With the electric eel, no muscular activity, or at least none comparable to this in extent, accompanies the discharge.

The circuit used in the measurements made on the first specimen is shown in Text-fig. 2. The fish rested on a metal sheet  $S_1$ , which was at ground potential. The wet ventral surface made good electric contact with this sheet. The smaller sheet  $S_2$  was shaped to cover the dorsal surface of the electric organ on one side of the fish, firm pressure and moisture making good electric contact here also. These electrodes were connected to the oscillograph, so that the voltage between them could be measured. By closing the switch  $K$  the variable resistance  $R$  could be connected across the organ so as to draw a current during its discharge. The resistance  $R$  being known and the potential difference  $V$  at the peak of the discharge being measured, then by Ohm's law the cur-



Text-fig. 3. Graph of peak voltage  $V$  against peak current  $I$ .

rent  $I$  at the peak of the discharge is given by the equation

$$V = IR$$

Also the peak power  $P$  supplied by the electric organ to the resistance is given by

$$P = VI$$

One set of measurements completed before the fish showed signs of fatigue, is given in Table I below.

TABLE I.

Peak Voltage, Current and Power with Various Resistances.

R	V	I	P
ohms	volts	amperes	watts
$\infty$ *	220	0	0
370	230	0.6	140
100	210	2.1	440
50	205	4.1	840
25	200	8.0	1600
12.5	170	13.6	2310

\* Open circuit.

That these data are not precise is clear enough from the fact that the peak voltage on open circuit was observed as less than that across a resistance of 370 ohms. Such irregularities are caused both by the inaccuracy of the observation and the variability of the fish.

It will be noticed that the power rises with falling resistance over all the range of the observations. The reason for this is that without prior experience with the species we failed to provide calibrated resistances low enough to develop the maximum power

of the discharge. But some inference beyond the observations may be made, as is illustrated in Text-figs. 3 and 4.

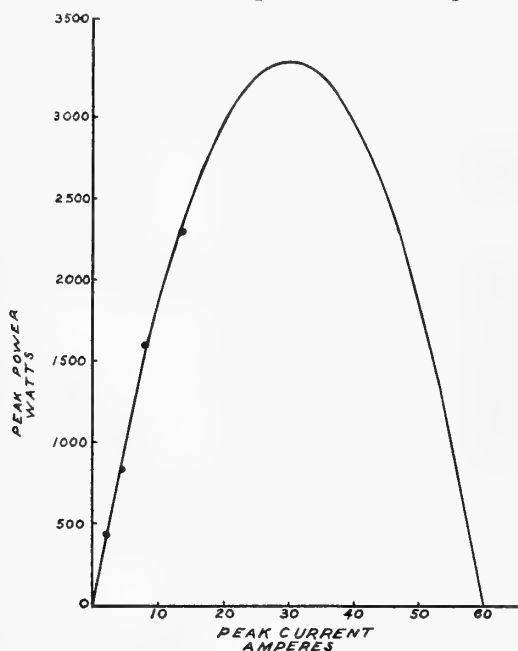
In Text-fig. 3 the values of  $V$  and  $I$  from Table I have been plotted and a straight line has been drawn among the plotted points. This construction may be justified by Ohm's law, and it is supported by many observations we have made on electric fish of other species. Values of  $V$  and  $I$  taken from this graph were used to compute the power  $P$  for the graph shown in 4, in which the plotted points again represent values from Table I.

The greatest current of which the organ is capable would be obtained by a complete short circuit, that is, by having  $R$ , and hence also  $V$  and  $P$ , practically zero. According to the graphs this current is 60 amperes. It is clear from the figures that the extrapolation is doubtful, since this value of the current is more than four times the highest reached in the observations. Probably, however, the organ is capable of a current of at least this order of magnitude. This does not mean that so great a current is normal to the fish. It is probable that the organ discharging in sea water carries something like half of its maximum current, since that would be the condition for the greatest release of power in the water.

For the maximum power Text-fig. 4 gives a value a little more than 3 kilowatts. The extrapolation here is more trustworthy than that for the maximum current, since this power is only 30 per cent. higher than the highest observed. Since the two electric organs discharge together, we have 6 kilowatts or about 8 horsepower as the electric power of both organs at the peak of the discharge. Of course it must not be overlooked that this is the peak power, and the average power, even during the discharge, would probably be some 25 or 30 per cent. of this. The average during a train of discharges would again be less than the average during one discharge, and would probably be 500 to 1,000 watts for both organs. Finally it should be noted that the trains of discharges do not appear to be given often.

The cross-sectional area of the organ on either side, in a plane parallel to the ventral surface, was about 250 square centimeters. The current was in a direction perpendicular to this plane, and its value for maximum power was, as shown above, about 30 amperes. Hence the current density at maximum power was about 0.12 ampere per square centimeter.

The mass of the organ on each side was about 2,000 grams. The maximum power released outside the organ being 3,000 watts, the maximum power per gram of the organ must have had an instantaneous value around 1.5 watts or one-third of a calorie per second.



Text-fig. 4. Graph of peak power  $P$  against peak current  $I$ .



## 6.

# The Ampulicidae and Sphecidae (Sphecinae) Taken at Kartabo and Other Localities in British Guiana.

(Hymenoptera).<sup>1</sup>

H. T. FERNALD.

(During the eight years of occupancy, by the Department of Tropical Research, of the New York Zoological Society's Station at Kartabo, British Guiana, extensive collections of insects were made. Most of these were taken in the quarter-mile area under intensive study—what may be called the Guiana Junglezone. Details and a general summary of this area may be found in "Studies of a Tropical Jungle," *Zoologica*, Vol. VI, No. 1.)

## INTRODUCTION.

The insects treated of in this paper were collected in British Guiana by members of the Tropical Research Station, New York Zoological Society, mainly at or near Kartabo. A few were taken at Arakaka on the Barima River in northern British Guiana; others at Mt. Everard on the Waini River; at Wismar on the west bank of the Demerara River; at Waratuk on the Potaro River below Kaieteur Falls; and at Lama Stopoff, just east of Georgetown.

While the Ampulicidae are few in number it is interesting to note that both species, described by Kohl, do not appear to have been recorded since, so far as literature available to the writer shows.

In the Sphecinae all four tribes are represented and as usual for tropical regions, the Chlorionini are the most abundant. That only four specimens of Sphecini are present is a little surprising as several others are liable to occur in this region.

Only one of three species of *Sceliphron* from this part of South America is represented, but twelve specimens indicate its abundance. No doubt further collecting in the northern and central portions of British Guiana will show the presence of other species of all the groups included in this paper.

## FAMILY AMPULICIDAE.

*Ampulex* Jurine.

Jurine, 1807. *Nouv. meth. de class. les Hymen.*, Pl. 14, p. 132.

*Ampulex sagax* Kohl.

Kohl, 1893. *Ann. des k.k. naturhist. Hofmus. Wien*, Vol. VIII, Hefts 3 & 4, pp. 477, 480.

Two female specimens, one from Kartabo, 28-V-1924; the other 24978 only. The only reference to this species is the original description where no locality is given. Kohl writes that he considers it a tropical species.

*Ampulex minor* Kohl.

Kohl, 1893. *Ann. des k.k. naturhist. Hofmus. Wien*, Vol. VIII, Hefts 3 & 4, p. 480.

One female from Kartabo, 21-V-1924. The only other reference is by Kohl whose specimen came from Brazil.

## FAMILY SPHECIDAE.

## Subfamily Sphecinae.

For many years this group was rated as a family but it has now been reduced to subfamily rank along with other former families.

The Sphecinae are divided into four tribes, the Podiini, Sceliphronini, Chlorionini and Sphecini. All four of these tribes are represented in this collection.

## Tribe Podiini.

*Podium* Fabricius.

Fabricius, 1804. *Syst. Piez.*, p. 183.

*Podium (Dynatus) nigripes* Westwood.

Westwood, 1832. *Griff. Anim. Kingd.*, Vol. XV, p. 516, fig. 3. (*Dynatus*).

One female, Kartabo, 29-III-1924. This species occurs from Mexico to Argentina.

<sup>1</sup> Contribution No. 635, Department of Tropical Research, New York Zoological Society.

***Podium (Trigonopsis) abdominale***  
Perty.

Perty, 1833. Delect. anim. artic. Brasil, p. 142, Pl. 27, fig. 18. (*Trigonopsis*).

Three specimens: one male from Kartabo, 9-VI-1924; a female, also from Kartabo, 5-IV-1922 and a female variety from Bartica District, 6-V-1922. This species is found from Guatemala to Brazil and Peru.

***Podium brevicolle* Kohl?**

Kohl, 1902. *Abhandl. d. k.k. zool-botan. Ges. Wien*, Vol. I, Heft 4, p. 62.

One male specimen, probably of this species, taken at Kartabo and labelled "Peach killer." This species is found from Mexico to Brazil.

***Podium gorianum* Lepeletier.**

Lepeletier, 1845. *Hist. nat. Ins., Hym.*, Vol. III, p. 324.

Sixteen specimens, all females; eleven from Kartabo, 23-VIII-1920; 24-VII-1922; 29-V, 3-VI, 11-VI, 15-VI, 28-VI, 1924; No. 22414; and two undated; Bartica District, 1, 2, and 3-VI-1924; 174; two without data. This species has been taken from Surinam to Brazil (Para).

**Tribe Sceliphronini.**

In this tribe only the genus *Sceliphron* is represented and that by only one species.

***Sceliphron* Klug.**

Klug, 1801. *Neu Schrift. Ges. naturf. Fr.* Berlin, Vol. III, p. 561.

***Sceliphron fistulare* Dahlbom.**

Dahlbom, 1843. *Hym. Eur.*, Vol. I, p. 22, no. 8. (*Pelopoëus*).

Twelve specimens, all females; Kartabo, 1919, 63, 20-VII-1922; 8, 4; No. 20859; Kalacoon, 1916 (2); Arakaka, 21-XII-1922 (2); Lama Stopoff, 14-X-1917; Kartabo, Hym.; no data, one specimen. This species is present in the neotropical region from Mexico to Paraguay (Argentina?).

**Tribe Chlorionini.**

This is the most abundantly represented tribe of the subfamily. Five divisions of the group, rated by some workers as genera, by others as subgenera, are recognized. The writer treats them here as subgenera, three of which are represented in this collection.

***Chlorion* Latreille.**

Latreille, 1802. *Hist. nat. Crust. & Ins.*, Vol. III, p. 333.

**Subgenus *Priononyx* Dahlbom.**

Dahlbom, 1845. *Hym. Eur.*, Vol. I, p. 439, No. 14.

***Chlorion (Priononyx) striatum* Smith.**

Smith, 1856. *Cat. Hym. Brit. Mus.*, Vol. IV, p. 266. (*Priononyx*).

One female specimen taken at Kartabo, IV-3-1926. Distribution — Nevada?; Arizona to Argentina.

**Subgenus *Isodontia* Patton.**

Patton, 1880. *Proc. Bost. Soc. Nat. Hist.*, Vol. XX, p. 380.

***Chlorion (Isodontia) costipennis***  
Spinola.

Spinola, 1851. *Mem. Acad. Sc. Torino*, Vol. XIII, p. 54, No. 35. (*Sphex*).

Four males and eight females. Males: Kartabo, 6-X-1921, 6-VI-1924; Mt. Everard, 15-XI-1922; Arakaka, 2-XII-1922; Females: Kartabo, 2-IV-1924, 3-VI-1924, 3-VII-1924; Bartica District, 20-IX-1917 (2); Penal Settlement; W. Bank Dem. R. 5-I-1923; Mt. Everard, 15-XI-1922. Distribution—Santo Domingo; Mexico to Brazil.

***Chlorion (Isodontia) dolosum* Kohl.**

Kohl, 1895. *Ann. des. k.k. naturh. Hofmus.*, Vol. X, Heft 1, p. 49.

Two female specimens taken at Kartabo, 21-V and 1-VI-1924.

From the literature available these specimens seem to be the only examples of this species captured since the one described by Kohl, recorded as from French Guiana, and they vary somewhat from his description. In one specimen the legs and petiole are entirely black, while in the other they are partly red. The abdomen, though partly red, has dark shades here and there, and the black hairs on the clypeus are large and almost bristle-like; elsewhere they are yellowish, almost golden in places.

These insects, while for the most part Isodontian in character, also possess some features like *Ammobia*. In one specimen there is an evident stigmal groove and the petiole is shorter and straighter than in most Isodontias. There seems to be what may be considered a rudimentary tarsal comb of seven short, stout spines much like those present in *Ch. (Isodontia) aztecum* to which this species also seems to be most closely related in general by its stout structure and petiole length. The form of the second cubital cell and the distance apart on the radial vein of the second and third transverse cubital veins compared with that between the second transverse cubital and the second recurrent veins on the cubital vein are typically Isodontian. Also the jaws do not each reach to the base of the other when closed, the two teeth being short.

This species may fairly be placed at the end of the series of *Isodontia* species, nearest to *Ch. (Isodontia) aztecum* on the one

hand and to *Ch. (Ammobia)* species on the other, much as *Ch. (Ammobia) lucae* is related to the other *Ammobias*. Kohl's specimen was recorded as from French Guiana.

**Subgenus *Ammobia* Billberg.**

***Chlorion (Ammobia) brasilianum* Sauss.**

Saussure, 1867. *Reise d. Novara, Zool.*, Vol. II, p. 39.

Four female specimens: Kalacoon, 1916, Hym. 25; W. Bank Dem. R., 9-II-1923; Waratuk, 16-II-1921; 29-IV-1924. This species occurs from Guatemala to Brazil.

***Chlorion (Ammobia) melanopum* Dahlbom.**

Dahlbom, 1843. *Hym. Eur.*, Vol. I, p. 27.

Eleven male specimens, taken at Kartabo, 29-II-1924; 1-III-1924; 10-V-1924; 24-V-1924; Trop. Research Station, New York Zool. Soc., No. 20900; No. 20550; Bartica, 27-V-1924 (2); Arakaka, 21-XII-1922 (2); one with no data. Reported from Brazil, only, heretofore.

***Chlorion (Ammobia) funestum* Kohl.**

Kohl, 1890. *Ann. des k.k. naturhist. Hofmus. Wien*, Vol. 5, Heft 3, p. 397.

Nine females represent this species in the collection. They were taken at Arakaka, 20-XII-1922; 21-XII-1922 (2); Trop. Research Station, New York Zool. Soc., No. 20960; Kartabo, 5-XI-1920; W. Bank Dem. R., 9-II-1923 and 29-III-1924. It has been reported from Brazil.

***Chlorion (Ammobia) neotropicum* Kohl.?**

Kohl, 1890, *Ann. des k.k. naturhist. Hofmus. Wien*, Vol. V, Heft 3, p. 222.

I have doubtfully referred four female specimens in this collection to this species as they more nearly agree with it than with any other.

Kalacoon, 1916, Bartica Dist., Br. Guiana, Hym. 71; Trop. Research Station, New York Zool. Soc., No. 21109; two without data. This species has been captured in Brazil.

***Chlorion (Ammobia) singularis* Smith.**

Smith, 1856. *Cat. Hym. Ins. Brit. Mus.*, Vol. IV, p. 261. (*Sphex*).

Two males and three females. Males: Kartabo, 1922; 1917 Penal Settlement Hym. 222; Females: Kartabo, 1922; Arakaka, 21-XII-1922 (2).

Distribution—Southern U. S.; West Indies; Mexico to Brazil.

In this interesting species the males may be entirely black with no ferruginous markings or they have such markings. Their presence with females of Cresson's *Ch.*

(*Ammobia*) *dubitatum* of which no certain males have been found, together with other facts of distribution, etc., makes it almost sure that these are the two sexes of *singularis*. In this lot the males have the ferruginous markings.

***Chlorion (Ammobia) ichneumoneum* Linnaeus.**

Linnaeus, 1758. *Syst. Nat.*, Ed. X, Vol. 1, p. 578, No. 27. (*Apis*).

The thirteen specimens in this collection are as follows. Male: Kartabo, 23-V-1924; Females: Kartabo, 201266, 201285, 21106, 12-V, 18-IV-1919; Bartica District, 28-V-1924 (2), 30-V-1924, 4-VI-1924, Hym. 125; two with no dates.

This widely dispersed and variable species is found in its typical form in the United States. Farther south, increase of the ferruginous of the petiole and abdomen, a darkening of the wings and variation of the amount of ferruginous on the legs have been recognized as marking varietal forms which at their extremes have been named.

The specimens in this collection are all varieties, but none of them has varied to such an extent as to become a named variety.

Distribution—North, Central and South America, at least as far as Brazil, with varieties in the warmer regions.

**Tribe Sphecini.**

***Sphex* Linnaeus.**

Linnaeus, 1758. *Syst. Nat.*, Ed. X, Vol. 1, p. 569.

The insects of this genus were for many years called *Ammophila*.

***Sphex abbreviatus* Fab.**

Fabricius, 1804. *Syst. Piez.*, p. 204. (*Pelopoeus*).

Five specimens of this species are in the collection. Males: Kartabo, No. 20700, 201283, W. Bank Dem. R., 5-I-1923, 1917 Penal Settlement, Hym. 28; Female: Kartabo, No. 20699.

This species occurs from Central America to Brazil.

***Sphex melanarius* Dahlb.**

Dahlbom, 1843. *Hym. Eur.*, Vol. I, p. 15. (*Ammophila*).

One male, Kartabo, 11-VI-1924. Distribution—South America; Brazil.

***Sphex muticus* Dahlb.**

Dahlbom, 1845. *Hym. Eur.*, Vol. I, p. 431. (*Ammophila*).

Two specimens. Male: Kalacoon, 1916, Hym. 300; Female: Kartabo, 29-III-1924. This species is reported from Brazil.

***Sphex opulentus* Guerin.**

Guerin, Duperry, 1830. Voy. Coquille, Zool., Vol. II, P. 2, p. 261. (*Ammophila*).

This large species, widely distributed in South America, is represented in this collec-

tion by five specimens. Male: Kartabo, No. 201135, 23-XI-20; Females: Kartabo, 1922; No. 201135, 23-XI-1929; 120. It has been recorded from Colombia to Paraguay, at least.

# 7.

## A *Résumé* of Mexican Snakes of the Genus *Tantilla*.

HOBART M. SMITH

Thirty-six species of *Tantilla* have been described or recorded (including the present article) from North America (with Mexico). Five of these have been synonymized with others (*bimaculata* with *calamarina*, *boulengeri* with *miniata*, *hallowelli* with *gracilis*, *kirnia* and *praeocula* with *fumiceps*). Of the remaining thirty-one, four may be eliminated as not belonging to *Tantilla*. *T. lintoni* and *brevissima* have been separated from this genus elsewhere (placed in *Tantillita*). *Tantilla depressa* is a synonym of *Geagras redimitus*.

*Tantilla nelsoni* Slevin (*Proc. Calif. Acad. Sci.*, ser. 4, vol. 15, 1926, pp. 200-201, María Madre Island, Nayarit, Mexico) is certainly not of this genus, differing from all other *Tantilla* in the possession of an undivided anal, entire nasal, 1-2 temporals, and white bands completely encircling a black body and tail. This combination of characters, together with absence of a loreal, and smooth scales in 15 rows, is unique in snakes, so far as I can determine. Accordingly, for this species I propose the generic name *Exelencophis*.<sup>1</sup>

The twenty-seven remaining North American species belong to five major species groups. These may be further subdivided, forming nine groups, some of which may again be subdivided. The ultimate process of subdivision into the smallest practical super-specific groups reveals fourteen divisions, as shown in the accompanying diagram. The characters of the groups and subdivisions follow.

I {	a {	1 { <i>moesta</i>
II {	b {	2 { <i>deppei</i>
		3 { <i>mexicana</i>
	c {	4 { <i>jani</i> <i>striata</i>

III {	d {	5 { <i>cuniculator</i> <i>phrenitica</i>
		6 { <i>deviatrix</i> <i>miniata</i> <i>rubra</i> <i>coronata</i> <i>wagneri</i>
	e {	7 { <i>wilcoxi</i> <i>rubricata</i>
		8 { <i>bocourti</i>
IV {	f {	9 { <i>canula</i>
	g {	10 { <i>calamarina</i> <i>martindelcampoi</i>
		11 { <i>gracilis</i>
V {	h {	12 { <i>nigriceps</i> <i>fumiceps</i>
		13 { <i>atriceps</i> <i>utahensis</i> <i>hobartsmithi</i>
	i {	14 { <i>planiceps</i> <i>eiseni</i> <i>yaquia</i>

- I. Belly black; collar very broad.
- II. Large bodied; ventrals not reduced; head not conical; lined.
  - b. Dark middorsal line; secondary temporal scale-like.
    2. Nuchal collar near parietal.
    3. Collar if present on posterior part of neck.
  - c. Light lined; secondary temporal elongate.
- III. Collared; body form as in II; not lined.
  - d. Secondary temporal elongate.
    5. Back dark, sharply differentiated from ventral color.
    6. Back dark or light but not sharply differentiated from ventral color.
    7. Posterior border of collar very narrow; black of head not emarginate behind eye.
  - e. Second temporal scale-like, broad or long.
- IV. Head conical; no collar; ventrals reduced; body short; temporal single or secondary temporal scale-like.
  - f. Supralabials normal, seven.
  - g. Supralabials reduced, six.
    10. Lined (three dark).
    11. Not lined.

<sup>1</sup> An effort was made to investigate more fully the characters of this curious species, but Dr. Slevin informs me that the type and only example known is lost.

- V. Light above; collar absent or poorly defined.
- h. Black head cap pointed behind; no evidence of a collar.
  - i. Black head cap straight edged posteriorly, a collar.
  13. Head cap extending 2-4 scales behind head, also below angle of mouth.
  14. Head cap extending 1-2 scales behind head, not to angle of mouth.

I am indebted to Dr. Thomas Barbour, Mr. Benjamin Shreve, Dr. Joseph R. Slevin and Dr. E. H. Taylor for loan of specimens and other assistance. A number of specimens were secured (including types of *wilcoxi rubricata*), and the entire study was completed, during tenure of the Walter Rathbone Bacon Traveling Scholarship.

Only diagnoses of Mexican species are given in the following. For diagnoses of United States species not here included, see Blanchard's synopsis (*Zool. Ser. Field Mus. Nat. Hist.*, vol. 20, 1938, pp. 369-376).

### *Tantilla atriceps* (Günther).

*Homalocranium atriceps* Günther, Biol. Centr. Amer., Rept., 1895, p. 146, pl. 52, fig. B.

*Tantilla atriceps* Amaral, Mem. Inst. Butantan, vol. 4, 1929, p. 218.

*Type Locality.* Nuevo León, Mexico.

*Diagnosis.* Body generally light above and below; a dark brown head cap, truncate posteriorly, extending one or one and a half scale lengths posterior to parietals; cap not extending below angle of mouth; a faint light collar covering about one scale length, not bordered posteriorly by a distinct black line; seven upper and lower labials; one preocular; two or rarely one postoculars; two elongate temporals, separating labials and parietal; prefrontals and labials separated; mental in contact with chinshields, rarely not (type); ventrals 123 to 158; caudals 55 to 70 (males 54 to 70, females 51 to 64).

*Mexican Localities.* Nuevo León (types, Brit. Mus.); 4 miles west of Saltillo, Coahuila (EHT-HMS 4555); 102 kilometers north of San Luis Potosí (EHT-HMS 23474-5).

*Specimens Examined.* Eight.

*Remarks.* Through the courtesy of Dr. Howard K. Gloyd I have been enabled to examine data on 50 specimens not seen by me, data for which were recorded by Dr. F. N. Blanchard. These show the existence of a great amount of variation in number of postoculars, ventrals and caudals. While variation in number of postoculars does not seem to have geographic correlation, the variations in ventral and caudal counts do have. The range of variation in ventral counts in males is 123 to 149; in females, 138 to 158. A comparison with the table of

variation given by Blanchard (*op. cit.*, p. 376) yields interesting results. In the nine forms (other than *atriceps*) listed by him, the maximum range of variation in males is 14, in females 23 (by error?). Since errors in determination of sex frequently occur in these small snakes, more significant is the range of both sexes combined; in *atriceps* it is 36, but in other forms it does not exceed 27. Most closely comparable to the range of variation in *atriceps* is that of *coronata* (including *wagneri*), which has range of 30. *T. atriceps*, having higher average counts than *coronata*, could be expected to have a greater range of variation, and does. Accordingly, the existence of two forms in *atriceps* is very strongly indicated. Unfortunately differentiation in ventral counts in *atriceps* is not accompanied by differences in color, as in *coronata*, nor is the area of intergradation between the two extremes of ventral counts as well defined in *atriceps* as in the latter.

The species rather obviously is in the process of either differentiation of two incipient subspecies (species), or of assimilation of two previously distinct species. It is difficult to know into which category *atriceps* should be placed. While the specimens from extremes of the range are easily distinguished, the character of the species in the broad area between (including northern Coahuila, western Texas) is not known except from a series from a single locality (Chisos Mts.). These exhibit no great range of variation (20, both sexes), but unfortunately straddle the middle of the range of counts for the whole species, so that some are very typical of Mexican specimens, others (the majority) typical of Arizona specimens (range 132 to 151). While it admittedly remains possible that two subspecies may be satisfactorily distinguished when larger series from more numerous localities are available, it does not seem practical to attempt subdivision of the species at present.

### *Tantilla bocourti* (Günther).

*Homalocranium bocourti* Günther, Biol. Centr. Amer., Rept., 1895, p. 149.

*Type Locality.* Guanajuato.

*Diagnosis.* Light above and below (young may be darker above, but this color shading into white of ventral surface); head black or dark brown above; first and fifth labials, and lower parts of other labials (except seventh) white; internasals white; a white nuchal collar covering one and one half scale lengths on nape, usually not involving tips of parietals, but bordering them; nuchal collar divided on midline or not; collar dark-bordered posteriorly by an area one scale in length or less; seven upper and lower labials; one preocular; two postoculars; two

temporals, the anterior elongate and in contact with postoculars, the posterior about as broad as long, scale-like; prefrontal separated from labials; first lower labials in contact medially, occasionally not; ventrals 164 to 185 (195?); caudals 46 to 61.

*Mexican Localities.* Known from the states of Jalisco (Magdalena, Guadalajara), Morelos (Cuernavaca, 8 kilometers north-east of Cuernavaca), Guanajuato (Guanajuato), Distrito Federal, Veracruz (Mirador), Guerrero (Omiteme), Puebla (22 kilometers north of Tehuacán, 10 miles northeast of Tehuacán), Michoacán (4 miles east of Tuxpam, between Zitácuaro and Río Tuxpam).

*Specimens Examined.* Thirty-one.

*Remarks.* As pointed out by Taylor & Smith (*Univ. Kans. Sci. Bull.*, vol. 25, 1939, p. 254), there is a discernible difference between eastern and western specimens in ventral, caudal and total counts. These indicated that two races are recognizable. However, further material has not borne out these supposed differences, but has shown that too great an overlap exists to permit separation. The counts are compared below.

		Ventrals	Caudals	Totals
males	western	165-180 (11)	52-65 (11)	219-244 (11)
	eastern	164-176 (4)	48-57 (4)	221-228 (4)
females	western	169-186 (12)	46-59 (12)	225-239 (12)
	eastern	166-173 (4)	46-52 (4)	216-221 (4)

### *Tantilla calamarina* Cope.

*Tantilla calamarina* Cope, *Proc. Acad. Nat. Sci. Phila.*, 1866, p. 320.

*Tantilla bimaculata* Cope, *Journ. Acad. Nat. Sci. Phila.*, ser. 2, vol. 7, 1875, p. 143 (Mazatlán, Sinaloa).

*Type Locality.* Guadalajara, Jalisco.

*Diagnosis.* Body light gray above, white below; three dark dorsal lines, the median spreading over most of top of head; lateral stripes on adjacent halves of third and fourth scale rows, extending onto head and not uniting with median dark area on head; six upper, six or seven lower labials; one preocular (rarely extremely minute and prefrontal entering eye), one postocular; one elongate temporal, in contact or not with postocular; prefrontals and labials separated or not; mental and chinshields in contact; ventrals 119 to 132; caudals 27 to 35.

*Mexican Localities.* Known from the states of Colima (Colima, Quesería, Tecmán), Distrito Federal (Santa Fé), Jalisco (Guadalajara), Morelos (4 miles south and 8 kilometers east of Cuernavaca), Nayarit (Sierra de Nayarit, San Blas, El Ocotillo), Puebla (Teziutlán) and Sinaloa (Mazatlán).

*Specimens Examined.* Six.

*Remarks.* This is related to *martindelcampoi*, which also has a dark-lined pattern, one temporal, degenerate head scales (fusion), and few ventrals and caudals. On the basis of lined pattern, *deppei* belongs with this group, but it has normal head scales.

### *Tantilla canula* Cope.

*Tantilla canula* Cope, *Journ. Acad. Nat. Sci. Phila.*, ser. 2, vol. 8, 1876, p. 144.

*Type Locality.* Yucatán.

*Diagnosis.* Body light gray above, stippled, white below; a middorsal light streak, not well defined; head reticulated, top lighter than sides; seven upper and seven lower labials; one preocular, two postoculars; two temporals, the anterior broad and scale-like (nearly as broad as long), the secondary more elongate; labials separated from parietals or not; prefrontals and labial separated; mental and chinshields in contact or not; ventrals 105 to 114, caudals 36 to 43.

*Mexican Localities.* Several specimens bear the locality datum "Yucatán." The only definite record is from Chichen Itza.

*Specimens Examined.* Four.

*Remarks.* As indicated by body form, shape of head, and low number of ventrals and caudals, the species appears to be related to *calamarina* and its allies. It is considerably different from the latter group in having the normal quota of head shields. It shows a great similarity to *vermiformis* of Central America.

### *Tantilla cuniculator* Smith.

*Tantilla moesta cuniculator* Smith, *Zool. Ser. Field Mus. Nat. Hist.*, vol. 24, 1939, pp. 32-34.

*Type Locality.* Mérida, Yucatán.

*Diagnosis.* Dark above, white below; a dark lateral area sharply differentiated from a somewhat lighter middorsal color and from white ventral surface; nuchal collar involving posterior tip of parietals; a very dim dorsolateral light stripe between lateral and dorsal areas; seven upper and lower labials; one preocular; two postoculars; two temporals, elongate, the anterior in contact with postoculars; prefrontals separated from labials; mental in contact with chinshields or not; ventrals 140 to 154; caudals 49 to 53.

*Mexican Localities.* Known only from the type locality.

*Specimens Examined.* One.

*Remarks.* This species may be related to *phrenitica*, with which its counts, and some details of coloration, compare well.

***Tantilla deppei* (Bocourt).**

*Homaloceranium deppei* Bocourt, Miss. Sci. Mex., Rept., 1883, pp. 584-585, pl. 36, fig. 11.

*Homaloceranium deppei* Günther, Biol. Centr. Amer., Rept., 1895, p. 151.

*Homaloceranium miniatum* Boulenger (nec Cope), Cat. Snakes Brit. Mus., vol. 3, 1896, p. 222.

*Type Locality.* Mexico.

*Diagnosis.* Pale brown, with a median and two lateral dark lines; a nuchal collar, complete except medially; ventral surface white; seven upper and lower labials; one preocular; two postoculars; two temporals separating labials from parietals, the secondary perhaps scale-like (see Bocourt's fig.); prefrontals and labials separated; mental in contact with chinshields; ventrals 147 to 152, caudals 55.

*Mexican Localities.* Known only from "southern Mexico."

*Specimens Examined.* None.

*Remarks.* The relationships of this form are difficult to determine. The lined pattern is suggestive of the *calamarina* group, but the scutellation and body form are different in all important respects. It most closely agrees with the *melanocephala* group, including *mexicana* and *armillata*. The small posterior temporal corresponds with this arrangement, but there is a nuchal collar, which does not occur in other members of the group (with a posterior neck collar).

***Tantilla deviatrrix* Barbour.**

*Tantilla deviatrrix* Barbour, Proc. Biol. Soc. Wash., vol. 29, 1916, p. 94.

*Type Locality.* San Luis Potosí, San Luis Potosí.

*Diagnosis.* Body light above and below, stippled above (said to be reddish in life); top of head light brown anteriorly, becoming black posteriorly; a white nuchal collar, involving tips of parietals, covering about two scale lengths, followed by a black border of about equal size; head cap extending laterally only to upper part of last labial, not reaching labial border posteriorly; upper labials white, sharply differentiated from dorsal color; an indentation of head cap behind eye, reaching to lower edge of upper preocular; seven upper and lower labials; one preocular; two postoculars; temporals elongate, the anterior in contact with postoculars; prefrontals and labials separated;

mental and chinshields separated; ventrals 154 to 160; caudals 63 to 66.

*Mexican Localities.* The type locality and Alvarez, San Luis Potosí.

*Specimens Examined.* One.

*Remarks.* This species is well differentiated from *bocourti* by the elongate secondary temporal. From *wilcoxi* it differs in the mental character (touching chinshields in *wilcoxi*), greater width of posterior black border of nuchal collar (one scale length or less in *wilcoxi*); and in various features of the coloration and the sides of the head.

***Tantilla hobartsmithi* Taylor.**

*Tantilla hobartsmithi* Taylor, Trans. Kans. Acad. Sci., vol. 39, 1937, pp. 340-342, fig. 2.

*Type Locality.* La Posa, ten miles northwest of Guaymas, Sonora.

*Diagnosis.* Body light above and below; a black cap on head, truncate and straight-edged posteriorly, extending about one scale length on nape; black of head not extending below angle of mouth onto gular scales; a very dim, narrow light collar one scale wide, or less, not dark-bordered posteriorly; a fine, but very distinct, middorsal black line; seven upper and lower labials; one preocular; one postocular (probably varies, one or two); anterior temporal relatively broad, but longer than broad, in contact with postocular; a secondary and also tertiary temporal; prefrontals separated from labials; mental separated from chinshields; ventrals 129, subcaudals 53.

*Mexican Localities.* Known only from the type locality.

*Specimens Examined.* One.

*Remarks.* Closely related to *atriceps*, which agrees in most characters of scutellation, and pattern. The latter also occasionally shows a faint middorsal dark line, which might appear more obvious (or not) in specimens dried as is the type of *hobartsmithi*. The latter is tentatively regarded as distinct through its possession of three temporals and the distinct middorsal black line, correlated with the fact that no *atriceps* have been collected near its type locality. Only further specimens will show whether these characters are invariable.

***Tantilla jani* (Günther).**

*Homaloceranium jani* Günther, Biol. Centr. Amer., Rept., 1895, p. 148, pl. 52, fig. D.

*Type Locality.* Guatemala.

*Diagnosis.* Ground color brown; three narrow, black-edged white lines, the median involving the vertebral scale row, the lateral stripes involving adjacent halves of the third and fourth scale rows; median stripes



sometimes not white, but brown, as ground color, but its dark edges evident; a complete nuchal collar, about one and one half scale rows wide, involving tips of parietals; seven labials; one preocular; two postoculars; two elongate temporals, anterior broader than posterior; ventrals 139 to 154, caudals 40 to 50 (in 22 specimens).

*Mexican Localities.* La Esperanza, Chiapas, and Tapanatepec, Oaxaca.

*Specimens Examined.* Twenty-two.

*Remarks.* The cotypes are two, one from Guatemala, the other from "Hacienda Rosa de Jericho, Nicaragua" (*vide* Boulenger, Cat. Snakes, vol. 3, 1896, p. 221; Günther says Matagalpa). The Nicaragua specimen has 136 ventrals, and no lateral light stripe, and accordingly I do not believe it is the same as the Guatemala specimen (the one figured by Günther) which I designate lectotype. The specimens from Finca El Ciprés, Volcán Zunil, Guatemala, reported by Slevin (*Proc. Calif. Acad. Sci.*, ser. 4, vol. 23, 1939, p. 411) as *fusca* I have seen and cannot differentiate from the Chiapas and Oaxaca specimens above mentioned.

*Comparisons.* The present species may be compared with those included by Boulenger in *trilineata* and *fusca*. Since the original descriptions indicate that his synonymies of these two are perhaps not wholly correct, *jani* is compared directly with the original descriptions.

*T. fusca* Bocourt, 1883 (Guatemala)—uniform light brown above, 137 ventrals, more than 34 caudals; Guatemala. Absence of all markings, including collar and longitudinal lines, does not describe *jani*. Boulenger's description of *fusca* says "Brown above, with or without a light, dark-edged lateral line, with or without a blackish vertebral line; head dark brown or blackish above, with yellow markings as in *H. melanocephalum*." This remarkable composite description is based upon the original description of *fusca*, two cotypes of *jani* (which apparently represent two species), and upon a specimen from Dueñas, Guatemala (this is the one with a dark vertebral stripe) referred by Günther to *armillatum*, but which is not that at all but possibly is the same as Günther's *mexicana* (or is an unnamed species). The specimen from Cartago, Costa Rica, referred by Boulenger to *melanocephala*, was apparently correctly allocated with *armillata* by Günther. The latter differs from South American *melanocephala* at least in ventral counts.

*T. trilineata* Peters, 1880 (Guatemala, Honduras)—lateral light stripe "running on the third scale row"; whole gular region apparently pigmented, at least the lower labials not heavily nor distinctively pig-

mented; no light internasal spot; ventrals 145; caudals 41.

*T. taeniata* Bocourt, 1883 (Guatemala)—median stripe continuous, covering at least a full scale width; dark borders not evident, nor dotted lines on fifth, sixth and first scale rows; lower labials not pigmented; stripes said to be half width of interspace (much less in *jani*); 149 ventrals; 68 caudals.

*T. trivittata* Müller, 1885 (Guatemala, Honduras)—said to have six upper labials.<sup>2</sup> Median stripe one and one-half scale rows wide, extending to end of tail; lateral stripes to middle of tail.

The species synonymized by Boulenger with *virgata* appear more distantly related, having the light lines and interspaces of about equal width.

### *Tantilla martindalcampoi* Taylor.

*Tantilla martindalcampoi* Taylor, *Trans. Kans. Acad. Sci.*, vol. 39, 1937, pp. 347-348, fig. 6.

*Type Locality.* El Treinta, Guerrero.

*Diagnosis.* Gray, with three broad, dark stripes on body and tail, the median one and two half scale rows wide, spatulate on head; lateral stripes on adjacent halves of fourth and fifth rows, connecting above eye with spatulate median stripe; six upper and seven lower labials; no preocular; one postocular; one elongate temporal, in contact with postocular; prefrontals broadly in contact with labials; mental in contact with chinshields; ventrals 114, subcaudals 39.

*Mexican Localities.* Known only from the type locality.

*Specimens Examined.* Two.

*Remarks.* Related to *calamarina* (see discussion).

### *Tantilla mexicana* (Günther).

*Elapomorphus mexicanum* Günther, *Ann. Mag. Nat. Hist.*, ser. 3, vol. 9, 1862, p. 57, pl. 9, fig. 1.

*Type Locality.* Mexico.

*Diagnosis.* Black head cap extending onto neck several scale lengths, followed by a light ring or a pair of spots; a middorsal dark line, and perhaps a lateral also; dorsal surface generally brown; dark area on head reaching to labial border below eye and at the seventh labial; seven upper and lower labials; one preocular; two postoculars; two temporals, the posterior scale-like (but

<sup>2</sup> Boulenger keys "*trilineata*" with the character of eight supralabials, and includes in his synonymy *trilineata* (described with seven), *taeniata* (described with seven) and *trivittata* (described with six). His only specimen (Bonacca Is., Honduras) was described by Günther as having seven supralabials. Specimens I have seen do not indicate the basis for such confusion.

slightly longer than broad); mental separated from chinshields; ventrals 158 to 159; caudals 44 to 52.

*Mexican Localities.* "Mexico."

*Specimens Examined.* None.

*Remarks.* Boulenger (Cat. Snakes, vol. 3, 1896, p. 216) concludes that the type (labelled Salle's collection) was not collected by Salle and is not from Mexico. There are facts, however, which indicate that it may actually have come from Mexico. Although the ventral count is matched by some South American specimens, it is lower than any Central American specimen related to *melanocephala* (i.e., *armillata*). Another specimen from Dueñas, Guatemala, referred by Boulenger (*op. cit.*, p. 221) to *fusca* and by Günther to *armillata* very closely matches the characters of *mexicana*, to which I have referred it. There is little doubt that these are distinct from *armillata*, and it is scarcely likely that they can be termed the same as the geographically distant *melanocephala*. In the absence of specimens in American museums it is at present impossible to determine its differential characters.

### *Tantilla miniata* Cope.

*Tantilla miniator* Cope, *Proc. Acad. Nat. Sci. Phila.*, 1863, p. 100.

*Tantilla miniata* Cope, *Bull. U. S. Nat. Mus.*, no. 32, 1887, p. 84 (corrects spelling of specific name, which he says was printed *miniator* by "errore typogr.").

*Homalocranium boulengeri* Günther, *Biol. Centr. Amer.*, 1895, pp. 148-149, pl. 52, fig. F (Huatusco, Veracruz).

*Type Locality.* Mirador, Veracruz.

*Diagnosis.* Dark reddish-brown above, the color shaded into that of white ventral surface on the first scale row; head black above; a nuchal collar involving tips of parietals, bordered behind by black, covering one to two scale lengths; seven upper and lower labials; one preocular; two postoculars; two elongate temporals, the anterior in contact with postoculars; prefrontals separated from labials; mental and chinshields in contact; ventrals 159 to 161; caudals 46 to 49 (plus a few).

*Mexican Localities.* Huatusco and Mirador, Veracruz.

*Specimens Examined.* One.

*Remarks.* Related to *phrenitica*. Gadow's *miniata* from Tezonapan (Teconapan, Texonapan), north of Ayutla, Guerrero, cannot be the same, but its identity is difficult to guess (*Proc. Zool. Soc. London*, 1905, p. 196). Boulenger's incorrect allocation of Cope's name (to *deppei*) accounts for the recognition of *boulengeri*.

### *Tantilla moesta* (Günther).

*Homalocranium moesta* Günther, *Ann. Mag. Nat. Hist.*, ser. 3, vol. 12, 1863, p. 352.

*Tantilla moesta* Cope, *Proc. Acad. Nat. Sci. Phila.*, 1866, p. 126.

*Type Locality.* Petén, Guatemala.

*Diagnosis.* Dark brown above, somewhat lighter but still heavily pigmented below; anterior part of head of same color as body; a very extensive nuchal collar involving over half of the parietals and laterally extending very nearly to the eye; seven upper and lower labials; one preocular; two postoculars; two temporals, not strongly elongate, the anterior in contact with postoculars; prefrontal in contact with labials; mental in contact with chinshields; ventrals 140 to 154; caudals 55 to 63.

*Mexican Localities.* Known from "Yucatán." Schmidt & Andrews' record for Mérida, Yucatán, refers to quite a different species (*cuniculator*).

*Specimens Examined.* Two.

*Remarks.* The species seems to have no very close relatives.

### *Tantilla nigriceps nigriceps* Kennicott.

*Tantilla nigriceps* Kennicott, *Proc. Acad. Nat. Sci. Phila.*, 1860, p. 328.

*Tantilla nigriceps nigriceps* Smith, *Copeia*, 1938, no. 3, pp. 149-150.

*Type Locality.* Fort Bliss, New Mexico.

*Diagnosis.* Body light above and below; a black head cap V-shaped posteriorly, the apex extending over three to five scale lengths on nape; seven upper and lower labials; one preocular; two postoculars; two temporals, both considerably longer than broad, neither extremely elongate; primary temporal in contact with postoculars or not; prefrontals separated from labials or not; mental usually separated from chinshields, occasionally not; ventrals 146 to 161, caudals 35 to 62.

*Mexican Localities.* Known only from Río Santa María, near Progreso, Chihuahua.

*Specimens Examined.* Sixteen.

*Remarks.* The present form, with *fumiceps*, is very distinct from any other species.

### *Tantilla nigriceps fumiceps* (Cope).

*Scolecophis fumiceps* Cope, *Proc. Acad. Nat. Sci. Phila.*, 1860, p. 371.

*Homalocranium praeoculum* Bocourt, *Miss. Sci. Mex.*, Rept., 1883, pp. 582-583, pl. 36, fig. 8 (Colorado).

*Tantilla kirnia* Blanchard, *Zool. Ser. Field Mus. Nat. Hist.*, vol. 20, 1938, pp. 373-374 (9 miles east of Pleasanton, Atascosa Co., Texas).

*Type Locality.* Unknown, restricted to that of *kirnia*, 9 miles east of Pleasanton, Atascosa Co., Texas.

*Diagnosis.* Body light above and below; a black head cap V-shaped posteriorly, the apex extending over three to five scale lengths on nape; seven upper and lower labials; one preocular (rarely two); two postoculars; two temporals, both considerably longer than broad, neither extremely elongate; primary temporal in contact with postoculars or not; prefrontals separated from labials or not; mental usually separated from chinshields, occasionally not; ventrals 130 to 150 (males 130 to 138, females 141 to 150); caudals 39 to 48 (males 43 to 48, females 39 to 44).

*Mexican Localities.* Recorded only from Mier, Tamaulipas.

*Specimens Examined.* Seven.

### *Tantilla phrenitica* sp. nov.

*Holotype.* U.S. National Museum No. 110381, female, collected at Cuautlapan, Veracruz, August, 1940. *Paratypes.* Twenty-five, including U.S.N.M. 110379-80, 110382-5, topotypes; U.S.N.M. 38134, Semacook (collected by Geo. P. Goll), Guatemala; U.S.N.M. 20835, Totontepec, Oaxaca; EHT-HMS 22367, El Limon Totalco, Veracruz; EHT-HMS 23561-70, 23572-76, 23582, topotypes.

*Diagnosis.* Dorsal surface dark, its color sharply differentiated from white or orange ventral surface; centers of lateral scales lighter than their edges; a nuchal collar, usually involving tips of parietals; snout dark; large postorbital light spot bordering edge of upper lip usually present; four anterior infralabials dark; seven upper and lower labials; one preocular; two postoculars; two elongate temporals, the posterior more elongate than the anterior, the latter in contact with postoculars; prefrontals separated from labials; mental and chinshields in contact; ventrals 135 to 147; caudals 36 to 42.

*Description of holotype.* Rostral about as high as broad, portion visible from above a little less than half its distance from frontal; internasals about half as long as prefrontals; length of frontal (1.9 mm.) greater than its width (1.5 mm.) or distance from tip of snout (1.8 mm.), or length of interparietal suture (1.7 mm.), less than maximum length of parietals (2.9 mm.); width of frontal about twice width of a supraocular (0.75 mm.); nasal completely divided, strongly indented below and somewhat less strongly above, anterior section broader than posterior section; preocular large, in contact with nasal; diameter of orbit (0.8 mm.) less than half its distance from tip of snout (2.0 mm.); two temporals, the secondary a little longer and narrower than primary; latter in contact with two postoculars (upper fused with supraocular

on one side, abnormal); seven supralabials, last much the largest, others not much different from each other in height; seven infralabials, fourth much the largest, four in contact with anterior chinshields; mental in contact with chinshields; posterior chinshields narrower than and about three-fifths the length of anterior pair.

Dorsals in 15 rows, smooth, not pitted; 137 ventrals; anal divided; 40 caudals; total length 175 mm.; tail 33 mm.

*Color.* Dorsal surface of head and body dark brown or black; color of head extending to labial border, except for a light spot (bordering lip) behind the eye, including the fifth supralabial and edges of adjacent scales; a light nuchal collar, involving tips of parietals and of secondary temporals, covering two scale lengths on the nape, somewhat broader laterally and including posterior half of seventh labial; body uniform dark, except that the centers of the scales are stippled lighter, visible only microscopically on most scales, but easily visible to the naked eye on first row of dorsals; dorsal pigment terminating abruptly at ends of ventrals; anterior portion of mental, and all of four anterior infralabials dark; remainder of infralabial border dark; remainder of ventral surfaces of body and tail unmarked; tail and posterior portion of body (ventrally) orange, brightest posteriorly, anteriorly becoming white.

*Variation.* In the twenty-five paratypes, one postocular occurs in three; 6-7 infralabials in three; 6-7 supralabials in one; ventrals 137 to 142, caudals 37 to 44 in twelve males, 135 to 147, and 36 to 42 in thirteen females. The nuchal collar involves the tips of the parietals in fifteen (barely in three), borders the parietals in ten; mental in contact with chinshields in all.

*Discussion.* This species is the same (apparently) as Boulenger's (Cat. Snakes, vol. 3, 1896, p. 222) Guatemala specimen referred to *schistosa*. It is not the same as Bocourt's *schistosa* (Miss. Sci. Mex., Rept., 1883, p. 585, pl. 36, fig. 10), however, described from Alta Vera Paz and Mexico. This species is described as having 121 ventrals (lowest *phrenitica* count is 135). This difference might be attributed to error in counting, except that *schistosa* is figured with a scale-like secondary temporal (always elongate in *phrenitica*), and completely without chin markings (mental and four anterior labials always dark in *phrenitica*).

The Mexican cotype of *schistosa* may belong to *phrenitica* (as I provisionally conclude), but if so it certainly is not the figured and described specimen, which must be considered the type and which probably is the Alta Vera Paz specimen.

***Tantilla rubra* Cope.**

*Tantilla rubra* Cope, *Journ. Acad. Nat. Sci. Phila.*, ser. 2, vol. 8, 1876, p. 144.

*Type Locality.* "Japana," Oaxaca (Tapana).

*Diagnosis.* Red (pink) above and below; snout, including internasals and half of prefrontals, white; rest of sides and top of head black, except for area involved in nuchal collar and a white circular area including the fifth labial and edges of adjacent scales; collar broad, including tips of parietals, extending anterolaterally to middle of seventh labial, extending posteriorly over two or three scale lengths; posterior border of collar black, extending over two or three scale lengths; seven upper and lower labials; one preocular; two postoculars; two elongate temporals, the anterior in contact with postoculars; prefrontals separated from labials, occasionally not; mental and chinshields in contact; ventrals 148 to 162, caudals 59 to 68.

*Mexican Localities.* Recorded from Santa Efigenia, Tapana, and various localities in the vicinity of Tehuantepec, Oaxaca; and 22 kilometers north of Tehuacán, Puebla. The British Museum specimen from Orizaba (Boulenger, *Cat. Snakes Brit. Mus.*, vol. 3, 1896, p. 219) does not seem to be *rubra*, nor can I allocate it with any other. It may be *bocourti*. Guanajuato records, of course, are incorrect.

*Specimens Examined.* Eleven.

***Tantilla striata* Dunn.**

*Tantilla striata* Dunn, *Amer. Mus. Nov.*, no. 314, 1928, p. 3.

*Type Locality.* Mixtequilla, Oaxaca.

*Diagnosis.* Three light lines on body, the median involving one and two half scale rows, the lateral involving adjacent halves of third and fourth rows; no nuchal collar, replaced by two rounded light spots involving tips of parietals; belly light; seven upper and six or seven lower labials; one preocular; two postoculars; two elongate temporals, the anterior broader than the posterior and in contact with postoculars; prefrontal separated from labials; mental in contact with chinshields; ventrals 157 to 165; caudals 34 to 42.

*Mexican Localities.* Known only from the vicinity of the type locality. Obviously related to *jani*.

*Specimens Examined.* Three.

***Tantilla wilcoxi wilcoxi* Stejneger.**

*Tantilla wilcoxi* Stejneger, *Proc. U. S. Nat. Mus.*, vol. 25, 1902, p. 156.

*Type Locality.* Ft. Huachuca, Arizona.

*Diagnosis.* Body light, above and below; head dark gray above and on sides as far as

lower border of eye; a lateral extension of head cap to labial border, including parts of sixth and seventh labials; black cap scarcely indented behind eye; snout pigmented; collar involving posterior tips of parietals, covering one to one and one-half scale lengths; a narrow black posterior border covering one scale length or less; seven upper and lower labials; one preocular; two postoculars; temporals elongate, the anterior in contact with postoculars; prefrontals and labials separated; mental and chinshields usually in contact, occasionally not; ventrals 149 to 164; caudals 62 to 69.

*Mexican Localities.* Mojaráchie, Chihuahua.

*Specimens Examined.* Six.

*Remarks.* This species is well differentiated from *bocourti*, which it resembles in color, by the shape of the secondary temporal. The narrow posterior border of the light collar, lack of sharp differentiation between white labial area and dark coloration of top of head, and absence of an indentation in the dark area behind eye differentiate this species from others of the group.

***Tantilla wilcoxi rubricata* subsp. nov.**

*Holotype.* U. S. National Museum No. 110399, male, fifteen miles southeast of Galeana, Nuevo León. *Paratypes.* U.S.N.M. No. 110398, topotype; E. H. Taylor - H. M. Smith No. 23473, Mt. Zapalinamé, Saltillo, Coahuila.

*Diagnosis.* Top of head dark gray, the color extending a little below level of eye, not very sharply differentiated from white of supralabial region; dark head color extending laterally to labial border on fifth and sixth supralabials; a narrow nuchal collar, covering little more than one scale length, involving tips of parietals (barely in one case); black border of nuchal collar very narrow, less than one scale length; head scales normal; ventrals 140 to 146; caudals 51 to 56; mental in contact with chinshields.

*Description of holotype.* Portion of rostral visible from above equal to length of internasals; latter little more than one-third length of prefrontals, about a fourth their size; frontal with four sides, two meeting in an obtuse anterior angle, sides curved, posterior angle acute; length of frontal (2 mm.) greater than its distance from tip of snout (1.8 mm.) or length of interparietal suture (1.6 mm.), much less than greatest length of parietal (2.9 mm.); maximum width of supraocular (0.9 mm.) more than half width of frontal (1.5 mm.); nasal apparently divided both above and below, naris pierced nearer upper edge than lower; anterior section of nasal larger and higher than posterior, which is elongate and in contact with preocular; two postoculars; two

elongate temporals, anterior in contact with postoculars; seven supralabials, last largest; seven infralabials, the first in contact with midventral line on one side; four labials in contact with anterior chinshields, one with posterior.

Scales in 15 rows throughout, smooth, not pitted; ventrals 140; anal divided; caudals 54.

*Color.* Dorsal surface brownish gray, stippled lightly; ventral surface white; head dark gray above, lighter on snout, the color extending on sides to below eye; head cap black around edges, extended laterally to labial border on portions of sixth and seventh supralabials; labial border white, not sharply differentiated from dark color; a small indentation of head cap behind eye, not reaching upper postocular; a narrow white nuchal collar of about one and one-half scale lengths, involving tips of parietals; collar bordered posteriorly by a narrow black band covering less than one scale length; lower labial border stippled.

*Variation.* The topotypic female is very similar in color, markings and scutellation. The mental is in contact with both anterior chinshields. Ventrals 146, caudals 51.

The specimen from Mt. Zapalinamé has six supralabials, the normal sixth and seventh fused; six infralabials on one side (second and third fused); nasal not divided above naris; nuchal collar barely involving extreme tips of parietals; some black stippling on some of the median belly scales; ventrals 144, caudals 56. The black posterior border of the nuchal collar is very narrow, nearly obsolete. Despite these numerous differences I believe this is the same as the Galeana specimens. It is obviously anomalous in some characters, and in addition has several of the posterior ventrals divided medially.

### *Tantilla yaquia* sp. nov.

*Holotype.* Museum of Comparative Zoology No. 43274, female, collected at Guasaremos, Río Mayo, Chihuahua, by H. S. Gentry, in August, 1936.

*Diagnosis.* Dorsal surface light brown, light below; head dark brown, black on sides and posteriorly, the cap extending about three scale lengths posterior to parietals; a faint nuchal collar, about one scale length, without a dark posterior border; a white area bordering lip behind eye, extending to middle of primary temporal; cap extending below angle of mouth; naris nearer upper than lower edge of nasal; latter divided above and below; ventrals 150, caudals 66.

*Description.* Length of portion of rostral visible from above about equal to length of internasals; latter a little less than half size of prefrontals; frontal hexagonal, anterior

angle obtuse, posterior angle a little less than right angle, sides slightly convergent posteriorly; frontal a little longer (2.2 mm.) than broad (1.8 mm.), longer than its distance from tip of snout (1.8 mm.), subequal to length of interparietal suture, considerably less than maximum length of parietal (3.2 mm.); maximum width of supraocular (0.9 mm.) no more than half width of frontal; naris pierced somewhat nearer upper than lower edge of nasal; posterior section of nasal about two-thirds size of anterior section, subequal to single preocular; two postoculars; two elongate temporals, the primary broader and in contact with postoculars; seven infralabials, fourth and fifth entering eye, 1-2-3-5-4-6-7 in order of increasing size, seventh much the largest; seven infralabials, four in contact with anterior chinshields; mental in contact with chinshields, the anterior pair of which is longer than the posterior.

Scales in 15 rows, smooth, not pitted; ventrals 150; caudals 66. Total length 240 mm.; tail 61 mm.

General ground color light brown above, clear below; top of head dark brown, tip of snout a little lighter; sides of head black, except lower parts of subocular and second labial, all of first, fifth and sixth labials, anterior half of seventh labial and lower half of primary temporal, all of which are cream-color; black on sides of head continuous with a black area extending posteriorly to cover about three scale lengths of neck; latter area extending laterally below corner of mouth onto first row of gulars, involving posterior half of seventh labial; posterior border of head cap straight on dorsal surface, curving forward on sides of head; a light collar about one scale wide, poorly defined, bordering head cap posteriorly, followed by brown stippling of the back, its posterior edge not otherwise marked; stippling on back light, most distinct at edges of scales; some stippling at ends of ventrals, and in gular region; ventral surface otherwise unmarked.

*Comparisons.* The present form is closely related to *eiseni* and *planiceps*. *T. eiseni* has the naris equidistant from upper and lower edges of nasal; ventrals more numerous (165 to 190); no light area behind eye, extending from labial border to middle of primary temporal; head flatter, snout more protruding. This and *yaquia* seem to be more closely related to each other than either is to *planiceps*, which has low ventral counts and nasal not divided above naris.

### KEY TO NORTH AMERICAN *Tantilla*.

1. Ventral surface heavily pigmented. *moesta*  
Ventral surface light, only extreme lateral tips of ventrals sometimes pigmented. .2
2. A lateral light stripe (a median also, but

- sometimes dim) at least anteriorly; no median middorsal dark stripe.....3
- No lateral light stripes; or, if present, a middorsal dark stripe also present....4
3. Two light spots on nuchal region, involving tips of parietals; ventrals 157 to 165, caudals 34 to 42.....*striata*
- A light nuchal collar, involving tips of parietals; ventrals 139 to 154, caudals 40 to 50.....*jani*
4. A lateral light stripe and a middorsal dark stripe; neck as well as head dark, collar (if present) crossing neck several scales back of head.....*mexicana*
- Not as described.....5
5. Body with three or five distinct dark stripes.....6
- Body not striped; or, if so, with only a median stripe.....8
6. A light nuchal collar (may be broken medially); seven supralabials; five dark lines on body.....*deppei*
- No light collar; six supralabials; three dark lines.....7
7. Lateral stripe on adjacent halves of fourth and fifth rows; no preocular; ventrals 114; caudals 39.....*martindelcampoi*
- Lateral stripe on adjacent halves of third and fourth rows; a preocular (sometimes very minute); ventrals 119 to 132; caudals 27 to 35.....*calamarina*
8. Dorsal surface of body dark and the dark color sharply differentiated from lighter ventral color at ends of ventrals.....9
- Dorsal surface of body dark or light, but if dark, the color not sharply differentiated from lighter ventral color at ends of ventrals.....10
9. Sides of body darker than middorsal area, the two areas rather sharply differentiated and separated by a dim, narrow, light line; ventrals 140 to 154; caudals 49 to 53.....*cuniculator*
- Sides of body not darker than nor distinctly differentiated from color of middorsum; ventrals 121 to 147; caudals 32 to 43.....*phrenitica*
10. Head of about same color as back or, if darker, its color not sharply differentiated from that of back; and no light nuchal collar.....11
- Head black or dark brown, sharply differentiated from color of back, or, a light nuchal collar present.....12
11. Sides of head of same color as top; a dorsal light stripe (in fresh material); seven supralabials; two postoculars; ventrals 105 to 114.....*canula*
- Labial border white, rather sharply differentiated from dorsal color of head; no dorsal light stripe; usually six supralabials; usually one postocular; ventrals 115 to 138.....*gracilis*
12. Black head cap V-shaped, its apex extending three to five scale lengths posterior to parietals on middorsal line; no nuchal collar; body light.....13
- Black head cap with a straight or slightly convex posterior margin; a nuchal collar at least faintly visible, not necessarily dark-edged behind; body dark or light.14
13. Ventrals in males 146 to 159, in females 150 to 161.....*nigriceps nigriceps*
- Ventrals in males 130 to 138, in females 141 to 150.....*nigriceps fumiceps*
14. Nuchal collar indistinct, of about one scale length, not dark-edged posteriorly (sometimes a few black dots).....15
- Nuchal collar very distinct, usually of more than one scale length, dark-edged posteriorly.....20
15. Black of head extending below angle of mouth onto gular scales, and posteriorly two or more scale lengths.....18
- Black of head not extending below angle of mouth onto gular scales, and posteriorly two or less scale lengths.....16
16. A fine, distinct, black, middorsal line; three temporals; ventrals 129 in type; usually (?) one postocular.....*hobartsmithi*
- No middorsal dark line; two elongate temporals; ventrals 127 to 160; usually two postoculars.....17
17. Ventrals in males 153 to 160, in females 163 to 172.....*utahensis*
- Ventrals fewer.....*atriceps*
18. Ventrals 134 to 141; nasal not divided above naris.....*planiceps*
- Ventrals more numerous; nasal divided above naris as well as below.....19
19. Ventrals 165 to 190; naris equidistant from upper and lower edge of nasal; no light area bordering lip behind eye and extending to middle of primary temporal.....*eiseni*
- Ventrals 150 in female type; naris much nearer upper than lower border of nasal; a light area bordering lip behind eye, extending to middle of primary temporal.....*yaquia*
20. Anterior temporal about as broad as long, scale-like.....*bocourti*
- Anterior temporal elongate, much longer than broad.....21
21. Posterior black border of nuchal collar covering one scale length or less....22
- Posterior black border of nuchal collar covering two or three scale lengths...23
22. Ventrals 149 to 164, caudals 62 to 69.....*wilcoxi wilcoxi*
- Ventrals 140 to 146, caudals 51 and 56.....*wilcoxi rubricata*
23. Black of dorsal surface of head not reaching labial border.....*deviatrix*
- Black of dorsal surface of head reaching labial border.....24
24. Nuchal collar covering two or three scale lengths, about as wide as its posterior border; snout white; dorsal and ventral surfaces pink.....*rubra*
- Nuchal collar much narrower, narrower than its posterior border; snout not white.....25
25. Ventrals in males 131 to 141, average 135; in females 139 to 148, average 143; caudals in males 42 to 51, average 46; in females 41 to 46, average 44; light band on back of head well defined although often interrupted on the midline.....*coronata coronata*
- Ventrals in males 119 to 129, average 127; in females 123 to 145, average 131; caudals in males 50 to 67, average 57, in females 41 to 59, average 51; light band on back of head usually more or less obliterated.....*coronata wagneri*



## 8.

# Eastern Pacific Expeditions of the New York Zoological Society. XXX.

## Atlantic and Pacific Fishes of the Genus *Dixonina*.<sup>1</sup>

WILLIAM BEEBE.

(Plates I & II).

[This is the thirtieth of a series of papers dealing with collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Eastern Pacific *Zaca* Expedition (1937-1938). For data on localities and dates of this expedition, refer to *Zoologica*, Vol. XXIII, No. 14, pp. 287-298.]

In connection with studies of differentiation or of identity in species of fish from opposite sides of North and Central America, I have reviewed the data on *Dixonina*. This consists of the published account by Fowler, of the type of *Dixonina nemoptera*, taken many years ago at Santo Domingo, West Indies, and of the second known Atlantic specimen by Metzelaar, from Puerto Cabello, Venezuela (not *Curacao*, as recorded by Dr. Myers.).

As regards Pacific records of *Dixonina*, Dr. George S. Myers, in 1936, searched the collections of the United States National Museum. He found a single individual of fifteen inches standard length, which long before had been acquired by the Museum, with no data except the locality Acapulco, Mexico. No description was published.

In the Japanese publication "Marine Fishes of the Pacific Coast of Mexico," 1937, with text by Yosio Hiyama, we are told in the preface that all the fish mentioned were collected in 1935-1936 on the trial fishing trip of a Japanese boat, and all taken by trawling. There are four lines of text on page 27 which refer very evidently to *Albula*, with the note that this species was "abundant in the Gulf of California." We

find, however, the single sentence, "in some specimens the last rays of dorsal elongated." In agreement with this, Plate Five presents an excellent colored figure of *Dixonina*, both as to correct relative length of the maxillary, number of lateral line scales and in the two elongate fin rays. So we must recognize this as the second Pacific published record of this species. The length of this specimen seems to have been 270 mm.

Along the northern part of the Pacific coast of Costa Rica, on the Eastern Pacific *Zaca* Expedition of the Department of Tropical Research, we rediscovered, in 1938, this interesting relation of the bonefish. At three places along a stretch of shore of about seventy-five miles we took a total of 19 *Dixonina*, both in seines and by hand line from the *Zaca*, the fish measuring from 80 to 365 mm. standard lengths.

The two Atlantic specimens measure 381 and 260 mm. standard lengths respectively. With the published data of these I have compared two of my Pacific *Dixonina*, one of 352 and the other 365 mm., and the accompanying table gives the comparative results. In the same table are corresponding characters of two additional Pacific *Dixonina*, of 185 and 80 mm. standard lengths.

### *Dixonina pacifica* sp. nov.

*Type*: Holotype, No. 26,131, Eastern Pacific *Zaca* Expedition of the Department of Tropical Research, New York Zoological Society; Port Culebra, Costa Rica (No. Lat. 10°31'; West Long. 85°40'): caught on hand line from the *Zaca*, January 24, 1938; standard length 352 mm.; adult female in full breeding condition. Type in the collections of the Department of Tropical Research, New York Zoological Society.

<sup>1</sup> Contribution No. 636, Department of Tropical Research, New York Zoological Society.

**Diagnosis:** The distinction between the Pacific *Dixonina pacifica* and the Atlantic *Dixonina nemoptera* is as follows. In the former there is a greater number of lateral line scales (81 to 84, as compared with 76); increased number of vertical lines of scales on dorsal half (11, not 9), and on ventral half (9, not 7); decrease in predorsal scales (22 instead of 30); smaller eye (6.8 to 7, not 4.15); longer pelvic fins (2.2 and not 2.7); greater number of gill-rakers (7 + 11 instead of 4 + 9).

Identical characters in *Dixonina* from the two oceans are, relative head length, depth, snout, maxillary, lengths of the first and last dorsal rays and the last anal ray, pectoral length, branchiostegals, and apparently fin counts, although as regards those of the dorsal and anal there is considerable confusion.

**Measurements and Counts:** Standard length 352 mm.; depth 80; head 120; eye 17; snout 44; maxillary 54; interorbital 18; pectoral length 54; pelvic length 54; snout to dorsal 195; snout to anal 330; snout to pectoral 117; snout to pelvic 247; dorsal height 60; last dorsal ray length 62; anal height 32; last anal ray length 40 mm.; dorsal fin count II, 20; anal fin count I, 9; pectoral count I, 16; pelvic count I, 10; gill-rakers 7-11; branchiostegals 14; lateral line scales 81; scale rows dorsal to lateral line 11; lateral line to anal 9.

**Range:** Northeastern Pacific coast Mexico: (Gulf of California and Acapulco); Costa Rica: (Potrero Grande, Port Culebra and Piedra Blanca Bays).

**Field Characters:** An elongate, spindle-shaped fish of the eastern Pacific coast, with conical snout overhanging the mouth; maxillary longer than snout; last ray of dorsal and of anal fin produced into a long filament; shining silver with dark scale lines along upper half of body. More than 80 lateral line scales.

**Color:** Brilliant silver, appearing dark above in certain lights with dark green on the head; this dorsal pigmentation resolves into eight very dark lines along each side of the upper half of the body, covering about one-fourth of each scale nearest to the adjoining line. Dorsal fin greenish, caudal dusky, anal silvery at base; a dusky spot at pectoral base, with yellow spot behind; basal membrane of pectoral apple green, rest of fin dusky. These colors fade at death. Iris silvery.

In the young fish, at least up to 90 mm. in length, two rows of dark spots extend along the side of the body, the upper close to the mid-back. In a 115 mm. fish the spots are less conspicuous and the dorsal dark lines begin to be distinct. The spots persist after death. In the full-grown fish the dark scale lines are fainter than in fish of medium size.

**Size:** The largest recorded fish is that in the U. S. National Museum collection, "a fine 15-inch adult," (381 mm.).

**Local Distribution:** Wherever we found these fish, they inhabited the same coastal shallows, off sand or muddy shores, as *Albula*.

**Abundance:** Common wherever found; twelve taken in one seine haul, and three and two on successive days with hand lines.

**Food:** A 90 mm. fish (28,051 b) taken at Potrero Grande, Costa Rica, had in its stomach 1 mysid, 1 shrimp and 1 euphausiid, all small. The food of another fish of 179 mm. from the same locality was an *Atherina* sp. of 40 mm. and an 80 mm. *Anchoviella* sp. The fully adult female (26,131) had, in its intestine, remains of a small fish and a small anomuran crustacean. In the stomach proper was a freshly swallowed and quite undamaged *Squilla hancocki*, the fifth known specimen.

**Breeding:** The type, specimen Number 26,131, standard length 352 mm. was taken by hand line from the *Zaca* in Port Culebra, Costa Rica, January 24, 1938. It proved to be a full-grown female with ovaries well developed. The eggs seem almost ready for deposition. The two ovaries are large, wrapped about the stomach and intestine, fairly thick down the mid-dorsal line of the coelom, and thinning out into sheets or wings around the caeca and stomach, almost meeting ventrally. They are 170 mm. in length and 30 mm. at their widest extent around the caeca. They weigh together 45 grams, and a carefully estimated count, based on divisional weight, works out at about 70,000 eggs. Individual eggs measure .35 to .45 mm. in diameter.

**Study Material:** 19 specimens. Costa Rica: Potrero Grande, 11 transitional adolescents (28,051, a, b, c, d, e; 26,046, a, b, c, d, e, f), 80-200 mm., 3 of which were in the immature spotted stage, seine; and 3 additional adolescents (26,123, 26,124 and 26,125), 220-270 mm., taken on hand line from *Zaca*, January 23, 1938. Culebra Bay, 2 adults (26,131, and one 26,131 a, lost after description), 352 and 365 mm., January 24, 1938, on hand line from *Zaca*; Piedra Blanca, 3 transitional adolescents (28,746 a, b, c), 80, 110 and 115 mm., all in spotted phase, February 2, 1938, seine.

**References:** *Dixonina nemoptera*, Myers, G. S. Copeia, 1936: 83-85 (Announcement of discovery of a Pacific *Dixonina* in the collections of the U. S. National Museum, labelled Acapulco).

*Albula vulpes* (in part) Kumada & Hiyama, Marine Fishes Pacific Coast of Mexico, 1937: 27, Plate 5 (short description, referring in part to *Dixonina*; Gulf of California, plate of *Dixonina*).



TABLE 1.

Comparison of proportions and counts of Atlantic *Dixonina nemoptera* and Pacific *Dixonina pacifica*.

	Atlantic		Pacific			
Standard length	381	260	352	365	185	80 mm.
Head length	109	108	120	115	52	23 mm.
Head (in length)	3.5	2.4	2.9	3.1	3.5	3.9
Depth (in length)	4.6		4.4	5	5	6.6
Dorsal fin	V, 16, I	19, I	II, 20		II, 20	II, 20
Anal fin	III, 6, I	7, I	I, 9		I, 9	I, 9
Pectoral fin	I, 16		I, 16		I, 16	I, 16
Pelvic fin	I, 8		I, 10		I, 10	I, 10
L.1. scales	76	76	81	84	84	80
Dorsal to L.1.	9	9	11	11	11	10
Anal to L.1.	7	7	9	9	9	9
Predorsal scales	30		22	22	23	23
Snout (in head)	2.6	2.5	2.7	2.6	2.6	2.7
Eye	5.6	5	7	6.8	5.7	4.6
Maxillary	2	2.1	2.2	2.1	2.2	2.1
Interorbital	4.15		6.6	5.1	4.7	
1st dorsal ray	1.8	1.9	2	1.8	1.8	
Last dorsal ray	1.7		1.9	1.5	2.6	5.3
Last anal ray	3.25		3		3.2	6
Pectoral length	2		2.2		2	2.1
Pelvic length	2.7		2.2		2.3	2.6
Gill-rakers	4+9		7+11	7+11	7+11	7+11
Branchiostegals	14		14		12	
Vertebrae					77	

ONTOGENETIC CHANGES.

The following are the ontogenetic changes apparent in this species, based on three individuals, a small transitional adolescent in the immature spotted phase of 80 mm., a late striped adolescent of 185 mm., and a fully breeding adult measuring 352 mm. in standard length.

The head increases slightly in comparison with the length, from young to adult, 3.9 times to 2.9; a corresponding change in depth is more marked, the increase being from 6.6 times to 4.4; The median fin count remains the same at all ages, although hints of two additional anterior spines in the anal were detected in a cleared 110 mm. adolescent; also in the same fish the pectoral count was distinctly increased to I,18 instead of the usual I,16, and the pelvic showed I,11 elements instead of the more typical I,10. The eye decreases relatively with age, measuring 4.6 times in the head in the youngest, as compared with 7 times in the oldest. The elongate last dorsal and anal rays increase markedly with age, the former changing from 5.3 to 1.9 times in the smallest and largest fish, and the anal filament from 6 to 3 times in the head. Ontogenetic changes in other characters are negligible.

MEDIAN FINS.

In regard to the moot question of whether the last two, closely associated rays of the dorsal and the anal fins should be counted as one, as one and a half, or as two seems to me to reduce itself automatically to a ques-

tion either of the recognition of natural evolution or of personal preference. My choice is to consider them as two rays.

In addition to any phylogenetic interest expressed in the elongated posterior ray of the median fins, it is an important differential generic character. It is also singularly persistent, although appearing sporadically in several genera of Isospondyli, such as *Tarpon*, *Dixonina*, *Dorosoma*, *Signalosa*, *Opisthonema* and *Chanos*. Thus if we should consider the posterior, closely-associated rays as one, we should have to describe the elongated character as formed by one-half of the posterior ray.

Judging by many metameral characters of these and other fish, and by general evolutionary knowledge, we know that phylogenetically, and often ontogenetically, such structures usually decrease in serial number. In the present case, we can be quite sure that the close association of the two posterior rays of the median fins is due to a comparatively recent reduction, and that at one time both were wholly separate as to subdermal elements. The same thing holds in the case of the present, intimately associated, but clearly distinguishable anterior spine or spines.

As these spines, present in both dorsal and anal fins, are extremely hard, and wholly lack the nodes or segments characterizing all rays, we must omit the conventional "Isospondyli"—Dorsal and anal without true spines."

In my discussion of the supporting bones of the median fins, instead of using the

cumbrous "proximal or distal interspinous bones," or "Pterygiophores", or "inter-neural and interhaemal bones", I am making use of Jordan's terms, *baseosts* and *axonosts*, which seem simple and self-explanatory.

#### ANAL FIN.

Based chiefly on a 185 mm. specimen, No. 28,046 b. With a few references to a 170 mm. fish (28,046 a), and to a 110 mm. fish (28,746).

The normal count of the anal fin in this species, both in fully adult breeding individuals, and in transitional adolescents from 200 down to 80 mm. standard lengths, is 1-9. In one specimen of 110 mm., however, I have found distinct traces of two minute spines anterior to the definite one which we count as I. No separate axonosts exist for the anterior four elements (the spine and three rays), although the anterior one flares out in a curved, double wing, and a distinct seam indicates that they, the next two, are fused together and to the distal head of the compound baseost. The first three baseosts (belonging to the spine and two rays) are fused at their distal ends, the second and third fanning out and forming the anterior and posterior edges of a large, thin, longitudinally oriented, bony wing or fan.

The 1st baseost (serving the spine) is a minute, bony nubbin (.8 mm.), attached to the anterior, distal portion of the 2nd baseost. The small hard spine (2.3 mm.) is closely applied to the anterior surface of the 1st ray. The 2nd baseost (2.5 mm.) forms the anterior border of the above-mentioned wing or fan; its ray is 6.5 mm. long. The 3rd baseost (6.5 mm.) forms the posterior border of the wing, and its ray which is the first branched one, is 14 mm. The 4th baseost is like all the succeeding ones, but its axonost is absent, the 4th ray articulating directly with the end of the baseost.

From here back, we find five baseosts, long, slender, but rather blunt, each fringed, fore and aft, by a fin or wing of thin bone. Each fin almost touches the one in front and that behind, so there can be extremely little inter-baseost movement, even if the muscular tissues permitted. Each baseost points sharply forward, the two last being even more acutely oblique, thus bringing the three posterior proximal tips close together. Each baseost articulates closely with its axonost. These are saddle-shaped, and each is partly covered with the pair of large, blunt spines which extends down and out from near the base of the rays.

The 8th ray, while furnished with normal axonost and baseost, is placed somewhat above the level of the rest of the rays, and its articular surface is at a greater distance from the corresponding surface of the axonost.

The 9th or last ray, the elongated one, ends basally in two, long, slender, curved spines which extend down toward, but do not quite bestride, the last axonost. This is almost double the size of the rest, and in all nearly grown or adult fish completely lacks a baseost. In a 110 mm. *Dixonina*, however, a faint, cartilaginous one is visible, one-third as long as the others. In this individual, too, both of the last two rays are elongate, and share equally in this generic character. They measure 7 mm. in length, compared with 4.3 mm. of the 7th ray.

The inter-rayal webbing is extremely delicate and is easily destroyed. From each side of each ray there arises a flap or narrow, vertical curtain of scales, attached only along the side, and hanging freely behind, about twice or three times as wide as the ray stem itself. Thus each ray possesses a web connecting it with the succeeding ray, and in addition, two longitudinal scale flaps which lie flat against the web, but can be lifted up at right angles and replaced again. The two posterior rays are wholly free from these scales, but the ray in front (7th in the anal) has three scales in a vertical line, forming its flap, and this number increases to a dozen or more along the long, anterior rays.

#### DORSAL FIN.

The count of the dorsal fin is consistent in both adult and young *Dixonina pacifica*, II-20. Except for its extra spine and nine additional rays, the dorsal fin is a replica of the description I have given of the anal fin.

In a 185 mm. fish the lengths of the elements are as follows: First spine, very small (1.5 mm.); 2nd spine 2.3 mm.; 1st ray, 6 mm.; 2nd ray, 12.3 mm.; 3rd ray, 21.3 mm.; 4th, or first branched ray, 28.6 mm.; 19th ray, 6.7 mm.; and 20th or elongate ray, 19.3 mm. in length.

#### GILL-ARCHES.

For gill-arch comparison I have chosen three individual fish, of 80, 185 and 352 mm. standard lengths, or approximately 25, 50 and 100 per cent. In the 80 mm. adolescent, the conventional gill-raker count of the first arch is 7-11, and in the 352 mm. fully adult individual it is the same, the anterior two or three on the hypobranchial being somewhat indistinct from a concentration of surrounding spinous areas. Of the rakers on the lower arch, the ceratobranchial bears 7, the hypobranchial the remaining 4. Most of the following notes have to do with these 7, as they are typical of those on all other segments.

In the smallest fish the 7 ceratobranchial rakers are the only armature on the outer side of this element, and are relatively long, straight-sided and covered solidly with long, sharp spines. Along the summit of the ridge

of this arch is a series of 6 narrow groups of spines, the profile view of the ridge resembling a jaw with wavy line of teeth. The inner side of the arch is a replica of the outer, 7-11, but with the individual rakers much smaller, and alternating with those on the outer side.

In the 185 mm. fish the rakers have become somewhat shorter and less erect, with the spines short, except those at the summit which are long and curved inward. The line of ridge spines has grown down, sending triangular areas over each side, alternating with the rakers proper. This stage is very similar to that found in the adults of some of the pike perches (*Stizostedion*).

Along the hypobranchial these form a closely interlocked pattern of alternating triangles. These almost fuse with the dental armature of the basibranchial. Along the periphery of this latter area the teeth are thick, sharp and peg-like, giving place almost at once to the rounded molars typical of the large areas of the oral cavity.

In the adult fish the rakers are short and thick, projecting only slightly above the level of the ridge, and with all the spines short. The descending areas have reached half way down the side of the arch, and below them, and between the bases of the rakers, new, small, spiniferous patches have developed. On the hypobranchial the patches are so continuous that only with difficulty can all 4 rakers be distinguished. In fact the adult arch is almost solidly covered with a spiny coat, out of which the original rakers project as low mounds.

Relative to the length of the fish, the rakers and gill-filaments are longer in the young than in the adult.

#### TEETH.

The teeth, as developed in an old transitional adolescent of 185 mm., are of two distinct types, first, sharp and curved ones, in rows or small clusters, but not villiform; and, second, low, blunt molar-like teeth in patches. The former are well-developed on the premaxillary and the mandible. In the young and half-grown fish they are in two distinct rows, but in the adults these become less apparent, and may merge into wider bands, 4 or 5 teeth deep. There is a slightly curved row of teeth on the vomer, which laterally merge into the narrow, elongate patches of the palatines.

In the back of the mouth, the 1st epibranchial shows only a very slight concentration into a patch, but on the 2nd, 3rd and 4th arches there are developed increasingly larger pharyngeal-epibranchial patches of teeth, all of the same type as those on the jaws. These, especially the ones on the 3rd and 4th arches, are directly opposed to the two large, triangular patches on the 5th ceratobranchials.

The molar type of teeth is segregated in mid-mouth, in three large, palatal patches, the central one on the parasphenoid, and the two lateral on the entopterygoids (not, as Fowler has them in his type description of *Dixonina nemoptera*, on the sphenoid and pterygoids). The tongue is fleshy with only the most minute rugosities. The 1st basibranchial is armed solidly with a great convex mass of the molars. The anterior half of the 3rd basibranchial is similar.

The two types of teeth are everywhere distinct in the 185 mm. fish, except on the 3rd basibranchial patch where they are intermediate, pointed, but much thicker and coarser than the jaw teeth. They are on their way to the change in the adult to the true molar type.

The opposite of this is seen in the full-grown fish, where a scattering of true molar teeth, intermediates, and typical gill-raker teeth are found intermingled, in intimate association in small patches on the hypobranchials of the 1st gill-arch. These are typical gill-raker patches, distinct from the large basibranchial molars. They seem to exhibit a distribution in reverse, secondarily outward and away from a dominant molar concentration.

Fish Number 28,051 b, a young transitional adolescent of 80 mm. has the entire edge of the premaxillaries toothed for a distance from the snout-tip back of 6.7, followed almost unbrokenly by a 2.8 mm. toothed edge of the maxillaries. On the latter there are only about twelve. The teeth on the premaxillaries and on the mandible are in two distinct rows, and distinguished by the decided divergence of the angles of direction, the first row almost straight, and those behind pointing obliquely back and into the mouth. The outer row is slightly larger and more even, but all are strongly curved and quite slender.

In front of the upper jaw, on the whole ventral surface of the snout, the skin is covered with minute but hard spicules.

The three palatal patches are fairly well defined in this young fish, rounded in outline and convex, but each tooth, although rounded, possesses a sharp point, while many of those along the outer rim of the palatines are curved and more slender, half-way between the two extremes of teeth.

About 1 mm. behind the symphysis of the upper jaw, lies the triangular vomer, its apex projecting forward, and the dentulous area confined to the posterior base. These vomerine teeth form a slightly irregular line, about 16 to 18 in all. They almost, but not quite, join on each side with the teeth of the palatines.

Adult female, No. 26,131, length 352 mm., has the premaxillaries toothed throughout, in about five rows in front, dwindling to one at posterior end. All are fairly slender,

slightly curved and sharp. All trace of teeth has gone from the edge of the maxillaries. The vomer has a straight line of teeth, slightly curved in front and containing about four rows. This area merges into the lateral palatine teeth, which form elongate areas, curved along outer outline, straight inside, four to six rows, narrowing behind to two. Teeth as in premaxillary but straighter.

Twenty-two mm. behind the vomerine teeth, begins the large, oval, median patch on the parasphenoid. This is 30 by 12 mm. On each side, also oval, but more elongate, with the inner margins almost touching the median patch, are the entopterygoid patches, 32 by 10 mm. The posterior end of the median area extends to between the second gill-arches, while the lateral patches cut into only the first arch. All three patches are decidedly convex. These teeth are molar-like, mosaics of low, smooth, rounded mounds, largest on the top of the convexities.

On the base of the tongue, covering the basibranchial, 18 mm. back of the fleshy tip, is a fourth molar patch, 9 by 16 mm., very steeply convex, sending back a narrow ridge over the center of the first arch, and ending on the third. This patch fits neatly into, and fills the space between, the three palatal patches, forming a most efficient grinding apparatus.

#### DIGESTIVE SYSTEM.

The oesophagus extends straight back from the pharynx for 40 mm. enlarging abruptly into the dead white stomach, a cylinder about 50 mm. long by 30 mm. in diameter. Posteriorly, this mid-section of the stomach narrows rather sharply into a long (50 mm.) tapering, blind finger. From the level of the oesophageal entrance, a large rounded diverticulum extends 35 mm. forward, with a diameter of 25 mm., lying directly over and ventral to the oesophagus. On the left side this forward extension of the stomach is exposed, its tissues distinguished by being darker than the stomach proper. Its top and entire right side, and most of the same side of the stomach as well, are covered solidly with the large, concentrically curved, white caeca. There are 15 main caeca, but 5 of these are bifurcated for one-fifth to one-half of their length. Each caecum is distinctly separated from its fellows by heavy bands of dark pigment. The attaching tissue is very slight, and the whole caecal mass readily peels away to its basal line of intestinal attachment.

From the summit of the anterior diverticulum, the intestine arises, extending straight back to the anus, a length of 145 mm., with the caeca occupying the first 60 mm. The lobes of the liver are very unequal, the left 65 by 25 mm. and the right 30 by 15 mm. The former extends around and down over the middle third of the stomach, to beyond the mid-ventral line, while the smaller lobe overlies the anterior caeca. The slight amount of fat, chiefly a linear mass along the ventral line of the caecum, is bright orange.

In a 90 mm. *Dixonina* (28,051 b) the stomach is relatively much more slender than in the adult, and the posterior blind end is not finger-like, but an undifferentiated posterior extent of the stomach, very slightly less in diameter. The caeca are 13 in number and relatively larger, both individually and in general extent. The anterior part of the stomach, the hardly distinguishable mid part and the entire posterior portion are all crammed with small mysids, shrimps and euphausiids.

#### ADIPOSE EYE-LID.

The adipose eye-lid was so loosely attached that a considerable number of sand grains had worked beneath it. With a little careful manipulation I got the entire mass off whole. It was attached most firmly anteriorly at the tip of the snout, below the nostril, and above the eye. In fact the anterior portion was attached while almost the whole posterior, much of the ventral and the postero-superior areas were loose.

#### EXPLANATION OF THE PLATES.

##### PLATE I.

- Fig. 1. *Dixonina pacifica*, sp. nov. Holotype, adult female, No. 26,131, Port Culebra, Costa Rica, January 24, 1938. Standard length 352 mm.
- Fig. 2. Outer right gill-arch of *Dixonina pacifica*, transitional adolescent. Standard length 80 mm.
- Fig. 3. Outer right gill-arch of *Dixonina pacifica*, transitional adolescent. Standard length 185 mm.

##### PLATE II.

- Fig. 4. Outer right gill arch of *Dixonina pacifica*, adult female, holotype. Standard length 352 mm.
- Fig. 5. Bend of outer right gill-arch of *Dixonina pacifica*, adult female, holotype. Standard length 352 mm.



FIG. 1.

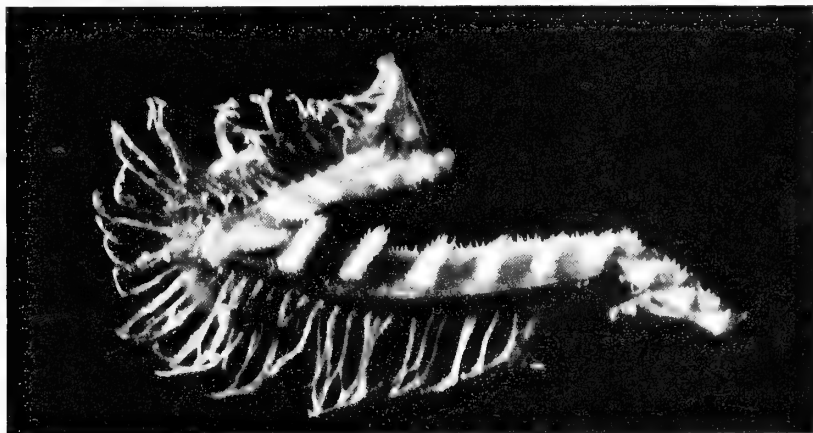


FIG. 2.

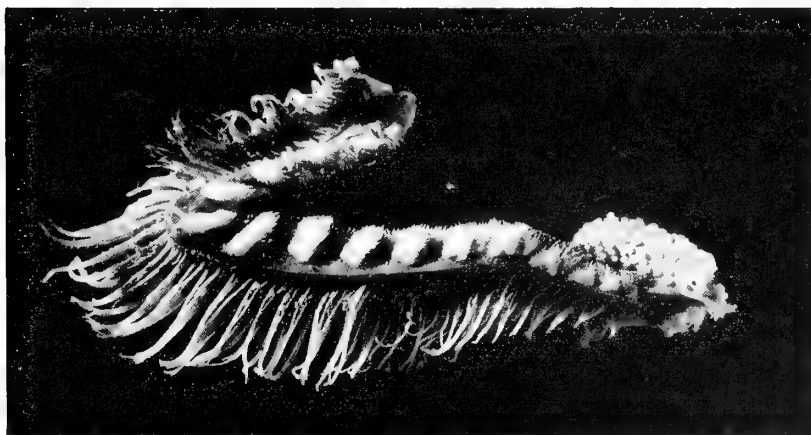


FIG. 3.

ATLANTIC AND PACIFIC FISHES OF THE GENUS *DIXONINA*.

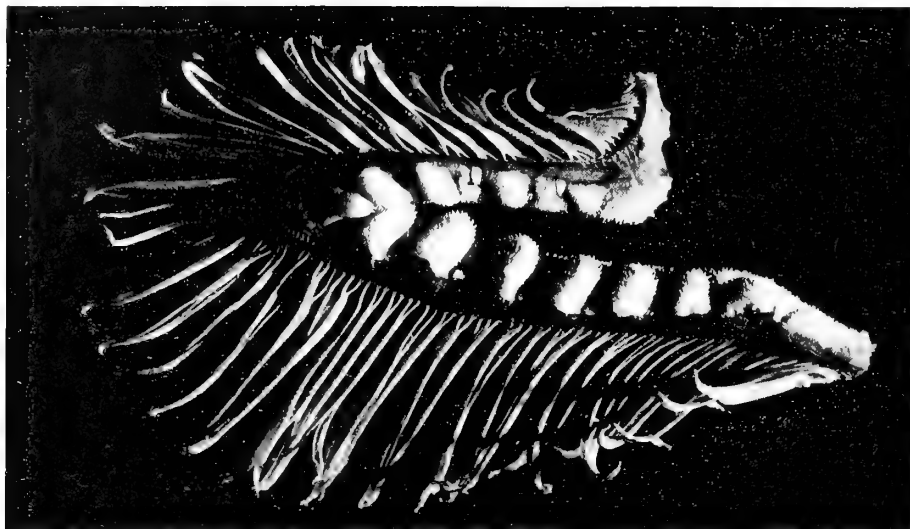


FIG. 4.

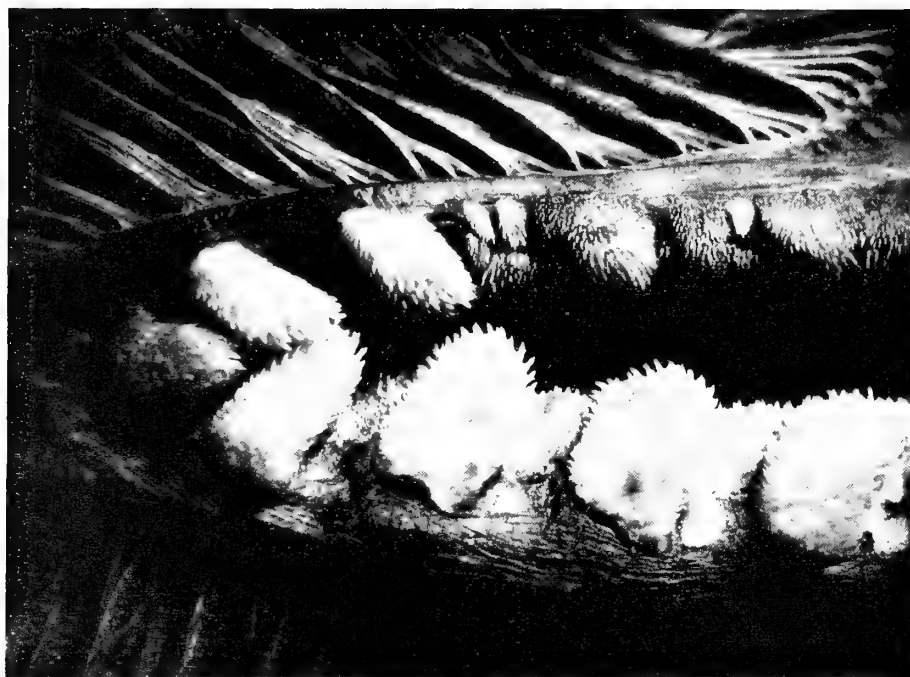


FIG. 5.

ATLANTIC AND PACIFIC FISHES OF THE GENUS *DIXONINA*.

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## 9.

## Notes on Tschudi's Types of Peruvian Birds.

HERBERT FRIEDMANN &amp; H. G. DEIGNAN\*

A little over a century ago, J. J. von Tschudi, the earliest important ornithological explorer of Peru, made a sizable collection of birds in that country. Among these specimens he found and described a large number of new forms, most of which are considered valid today. His collection went to the Museum of Neuchatel, Switzerland, from which institution, in 1866, the United States National Museum received 27 specimens of birds, mostly mounted—the conignment being marked "Types of Tschudi's Fauna Peruana." We have recently rediscovered these birds scattered through the collections and have made use of the occasion to go over them carefully.

We find that most of them must be regarded as types, or at least as cotypes. Tschudi described his new forms in the *Archiv für Naturgeschichte*, 1843 and 1844, and in his "Untersuchungen über die Fauna Peruana," 1844-46. In no case did he designate a definite specimen as the type or even intimate whether he had one or more specimens before him, or state an explicit, restricted, type locality. Inasmuch as his descriptions were all written after his collecting work was complete, it is reasonable to assume that all his birds were available to him at the time of his studies and that, therefore, in the absence of true holotypes, all of his paratypes (which would include all of his original series) must be considered as cotypes, except where the description, for one reason or another, does not fit a particular specimen.

Berlepsch & Hellmayr (*Journ. für Orn.*, 1905, pp. 6-20) reported on Tschudi's types in the museum at Neuchatel, apparently unaware of the fact that a considerable number of specimens had been sent away many years before. In fact, they merely discussed the Tschudi types they found at Neuchatel and made no comment on the forms described by Tschudi but no longer to be found there. The birds now in the United States National Museum fill in a good number of these omissions as well as revealing a number of cotypes of the forms still repre-

sented (in 1905) in Neuchatel. The specimens now in Washington, which we consider to be of type or cotype status, are listed below. Our specimens of forms which Berlepsch & Hellmayr found to be represented (by "type"—only three!) at Neuchatel in 1905 are considered cotypes; those which they failed to find at Neuchatel are, in lieu of other known specimens, considered to be types. If other specimens should be found in other museums, some of the types herein listed would, of course, become cotypes.

*Penelope adspersa* Tschudi =*Ortalis guttata adspersa* (Tschudi).

*Archiv für Naturgeschichte*, ix, (1), 1843, 386 (Peru, "frequenter in sylvis"; = eastern Peru).

Type: U. S. Nat. Mus. 41932; Perou.

Chapman (*Bull.* 117, *U. S. Nat. Mus.*, 1921, 44) writes that two males from Rio Cosireni have the throat and breast darker with the margins of the feathers whiter and more clearly defined than in examples from southeastern Colombia; and that, if the difference should prove to be constant, they should be known as *O. g. adspersus*. One of these Rio Cosireni birds is before us and agrees quite well with the unsexed type, except in having the upperparts more olive, less reddish-brown, and in being larger. The measurements of the two are as follows: type, unsexed, wing 185, tail 206, culmen from base 21 mm; Rio Cosireni, ♂, wing 203, tail 211, culmen from base 24 mm.

The type has the entire underparts slightly more brownish than the Rio Cosireni example, but its general brownishness may be partly due to foxing.

*Charadrius Winterfeldi* Tschudi =*Aphriza virgata* (Gmelin).

*Archiv für Naturgeschichte*, ix, 1843, 388 ("in Oceani Magni littoribus").

Type: U. S. Nat. Mus. 41933; original label lost, but locality entered in catalogue in 1866 as Valparaiso.

That Valparaiso, Chile, may be the actual type locality is not to be ruled out of consideration, as in his "Travels in Peru, Dur-

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ing the Years 1838-1842" (transl. by Thomasina Ross, 1849, p. 25), Tschudi describes birds seen for sale and at large in the harbor of Valparaiso on his way north to Peru, and he may have obtained his specimen of the surf bird there. The type is a bird in winter plumage and has the following dimensions: wing 162, tail 58, culmen from the base 26 mm.

***Columba frenata* Tschudi =**

***Oreopeleia bourcierii frenata* (Tschudi).**

*Archiv für Naturgeschichte*, ix, (1), 1843, 386 ("in sylvis Antium declivitatis orientalis," Peru = eastern slopes of the Andes of Peru).

*Type*: U. S. Nat. Mus. 41931, unsexed; Perou; Wing 160.5, tail 94.5, culmen from base 21 mm.

The type is somewhat foxed. It has been compared with a male from Rio San Miguel, Peru, from which it differs in being more rufescent above, the rump and tail lighter and brighter, and in having the breast paler, much less grayish, more of a pale cinnamon drab and the sides, flanks, and under tail coverts much more rufescent. In his description of *O. b. subgrisea*, Chapman (*Amer. Mus. Novit.* no. 31, 1922, p. 2) refers to the underparts of his new form, "... as in *O. frenata*, the breast pale drab-gray instead of cinnamon-drab or drab; center of abdomen slightly paler than breast, pale smoke-gray rather than drab as in most specimens of *bourcierii*; lower tail-coverts grayer." This is rather confusing, as the type of *frenata* is the brownest of all on the underparts. The Rio San Miguel bird, which was identified as *frenata* by Chapman (*Bull.* 117 U. S. Nat. Mus., 1921, p. 47) is intermediate between typical *bourcierii* (from El Roble and Almaguer, Colombia, and Zaruma, Ecuador) and the type of *frenata*. We have seen no specimens of *subgrisea* and can only call attention to the possibility of its range extending southward to northern Peru, making the Rio San Miguel specimen within its limits of variation, or the possibility of northern Peru and southwestern Ecuador being inhabited by variable intergrades between typical *bourcierii* and *frenata*, not constant enough to warrant nomenclatural standing.

***Columba meloda* Tschudi =**

***Zenaida asiatica meloda* (Tschudi).**

*Archiv für Naturgeschichte*, ix, (1), 1843, 385 ("frequenter in regionibus calidis praecipue declivitatis Antium occidentalis" = western slopes of the Andes in Peru).

*Type*: U. S. Nat. Mus. 41930, unsexed; Perou; wing 177, tail 125, culmen from base 27.5 mm.

***Conurus mitratus* Tschudi =**

***Aratinga mitrata mitrata* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 304 (Peru = Chanchamayo Valley; Zimmer, *Field Mus. Nat. Hist. Publ. Zool.*, ser. xvii, 1930, 263).

*Type*: U. S. Nat. Mus. 41926, unsexed; Perou; wing 189, tail 151, culmen from cere 31.5 mm.

***Conurus rupicola* Tschudi =**

***Pyrrhura rupicola* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 304 (Peru).

*Cotype*: U. S. Nat. Mus. 41925, dismounted specimen, unsexed; "Perou"; wing 133, tail 100+, culmen from cere 16 mm.

Another cotype is in the British Museum (*Cat. Birds Brit. Mus.*, xx, 1891, 225).

In his account of his journey, Tschudi (*Travels in Peru*, transl. by Thomasina Ross, 1849, p. 176) states that he found this bird together with the next one, abounding in the coastal region south of Lima, which may be taken as a more restricted type locality. The pose of the present (dismounted) specimen agrees with that in the figure of Tschudi's *Untersuchungen Ueber die Fauna Peruana* (Pl. 26, fig. 1).

***Psittacus tumultuosus* Tschudi =**

***Pionus tumultuosus* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 304 (Peru).

*Type*: U. S. Nat. Mus. 41927, dismounted bird, unsexed; Perou; wing 171, tail 79, culmen from cere 26 mm.

The type locality may be more definitely stated as the coastal region south of Lima, where Tschudi writes (*Travels in Peru*, transl. by Thomasina Ross, 1849, p. 176) he found this parrot to abound "... in the valleys along the coast," and to "... commit great depredations in the maize fields."

***Psittacus mercenarius* Tschudi =**

***Amazona mercenaria mercenaria* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 303 (Peru).

*Type*: U. S. Nat. Mus. 41928, unsexed; Perou; wing 198, tail 93, culmen from cere 30 mm.

***Caprimulgus ocellatus* Tschudi =**

***Nyctiphrynus ocellatus ocellatus* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 268 (Peru).

*Type*: U. S. Nat. Mus. 41912, unsexed; Perou; wing 131.5, tail 122, culmen from base 20.5 mm.

Peters (*Check-list Birds World*, iv, 1940,

196) considers *brunnescens* Griscom & Greenway to need confirmation before recognizing it. We have a single Brazilian bird which by locality may be either *brunnescens* or *ocellatus* and find it to be dusker than the type of *ocellatus* as it should be according to Griscom & Greenway if it were *brunnescens* but otherwise it disagrees with their description, being brighter, more rufescent brown than *ocellatus*. These writers state that *brunnescens* has a general light chocolate brown coloration while *ocellatus* is bright rufous brown. The reverse is true of the two birds before us. The birds are of comparable antiquity, the Brazilian specimen being from the U. S. Exploring Expedition's collection, so there should be no differential foxing. The validity of *brunnescens* is therefore very doubtful, as individual variation seems to be greater than was supposed.

***Capito glaucogularis* Tschudi =  
*Capito versicolor glaucogularis* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 301 (Peru).

*Cotype*: U. S. Nat. Mus. 41920, unsexed (female by plumage); Perou; wing 71.5, tail 81, culmen from base 22 mm.

While there seems to be no reason to consider this specimen as less likely a type than the others, it should be noted that in some details it agrees only approximately with the colored plate (plate 24, fig. 2 in Tschudi's *Untersuchungen Ueber die Fauna Peruana*). Thus, in the plate the crimson pectoral band extends entirely across the posterior end of the blue throat whereas in the specimen before us it is not quite so extensive; the green of the upperparts is lighter, slightly more yellowish in the bird than in the plate and the centers of the upper wing coverts not as dark as in the figure. The specimen, which is a "taken down" mounted specimen may, of course, have faded somewhat. It is also possible that the plate was made from another specimen, which is our reason for calling our bird a cotype.

A female of *versicolor* from Idma, Peru, is very similar to the type of *glaucogularis* and differs only in having the crown and occiput less yellowish and the yellow margin of the upper and posterior edges of the auricular area more distinct.

***Chamaeza olivacea* Tschudi =  
*Chamaeza brevicauda olivacea* Tschudi.**

*Archiv für Naturgeschichte*, x, (1), 1844, 279 (Peru; restricted by Hellmayr, *Cat. Birds Amer.*, iii, 1924, 293, to Montaña de Vitoc, Dept. Junin, Peru).

*Type*: U. S. Nat. Mus. 41916, unsexed,

dismounted bird; "Perou"; wing 96.5, tail 65.5, culmen from base 22.5 mm.

***Anabates montanus* Tschudi =  
*Anabacerthia striaticollis montanus* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 295 (Peru; = wooded region of Peru, between 10° and 12° South Lat.).

*Cotype*: U. S. Nat. Mus. 41923, unsexed, dismounted bird; "Perou"; wing 90, tail 75, culmen from base 17 mm.

Other cotypes exist in Neuchatel, and in the British Museum (Sclater, *Proc. Zool. Soc. Lond.*, 1871, p. 86).

In identifying the specimen we follow the nomenclature of Bangs (*Bull. Mus. Comp. Zool.*, lxx, 1930, p. 252) rather than of Hellmayr (*Cat. Birds Amer.*, iv, 1925, 195).

***Anabates ochrolaemus* Tschudi =  
*Automolus ochrolaemus ochrolaemus* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 295 (Peru = forest region of Peru, between 10° and 12° South Lat.).

*Cotype*: U. S. Nat. Mus. 41915, unsexed, dismounted bird; "Perou"; wing 83, tail 74, culmen from base 22 mm.

Other cotypes are in the British Museum and the Museum at Neuchatel.

***Dendrocolaptes chunchotambo* Tschudi  
= *Xiphorhynchus chunchotambo chunchotambo* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 295 (Peru = Chanchamayo Valley, Peru).

*Cotype*: U. S. Nat. Mus. 41918, unsexed, dismounted bird; "Perou"; wing 103, tail 90, culmen from base 35 mm.

Other cotypes exist in the Neuchatel and British Museums.

The present specimen has been discussed by Zimmer (*Amer. Mus. Novit.* no. 756, 1934, p. 17).

***Elaenia viridiflava* Tschudi =  
*Tyranniscus viridiflavus* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 274 (Peru = "coast region of Peru," errore = tropical zone of central Peru).

*Cotype*: U. S. Nat. Mus. 41921, unsexed, dismounted bird; "Perou"; wing 58, tail 48.5, culmen from base 9.5 mm.

There is another cotype in the museum at Neuchatel (referred to as the type by Hellmayr, *Cat. Birds Amer.*, v, 1927, p. 474).

This specimen is paler above, the feathers without the darker centers, when compared with Tschudi's colored figure (*Untersuchungen Ueber die Fauna Peruana*, pl. ix, fig. 2).

***Leptopogon superciliaris* Tschudi =  
*Leptopogon superciliaris superciliaris*  
Tschudi.**

*Archiv für Naturgeschichte*, x, (1), 1844, 275  
(Peru = fringes of the forests of central  
Peru, — Montaña of Vitoc, Dept. Junin, Hell-  
mayr, Cat. Birds Amer., v, 1927, p. 485).

*Type*: U. S. Nat. Mus. 41917, unsexed,  
dismounted bird; "Perou"; wing 75, tail  
63.5, culmen from base 14.5 mm.

***Pipra chloromeros* Tschudi =  
*Pipra chloromeros* Tschudi.**

*Archiv für Naturgeschichte*, x, (1), 1844, 271  
(Peru = montañas of "northwestern" Peru;  
= valley of Vitoc, Dept. Junin; Hellmayr,  
Cat. Birds Amer., v, 1927, 25).

*Type*: U. S. Nat. Mus. 41924, unsexed  
(adult male by plumage), dismounted bird;  
Perou; wing 59, tail 24, culmen from base  
10.5 mm.

***Cyphorhinus thoracicus* Tschudi =  
*Leucolepis thoracica thoracica*  
(Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 282  
(Peru = montañas of Uchubamba, near Vitoc,  
Dept. Junin).

*Cotype*: U. S. Nat. Mus. 41922, unsexed,  
dismounted bird; Perou; wing 68, tail 48,  
upper mandible broken.

This specimen is listed as a cotype rather  
than as a type because Hellmayr (Cat. Birds  
Amer., vii, 1934, p. 287) writes "(type in  
Neuchatel Museum)." Yet, Berlepsch &  
Hellmayr (*Journ. für Orn.*, 1905, 6-20), in  
their paper on the Tschudi types at Neu-  
chatel, do not list this species.

Tschudi's colored figure (Untersuchungen  
Ueber die Fauna Peruana, 1846, pl. 16, fig.  
1) is very poor. The type has the face, chin,  
throat, and breast much more rufescent and  
much brighter than the published figure.

***Ptilogonys leucotis* Tschudi =  
*Entomodestes leucotis* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 270  
(Peru).

*Cotype*: U. S. Nat. Mus. 41908, unsexed,  
dismounted bird; Perou; wing 106.5, tail  
106, culmen from base 21 mm.

Baird (Rev. Amer. Birds, pt. 1, 1866,  
p. 432-433) has described this specimen in  
detail. He writes that the bird is one "... of  
Mr. Tschudi's types, presented to the  
[Smithsonian] Institution by the Museum  
of Neuchatel. It is moulting a considerable  
portion of its feathers, which somewhat ob-  
scures its characters, and it may even be a  
young bird not yet arrived at maturity." It  
does not seem probable that the specimen  
is immature. It apparently is an adult in  
moult, especially on the chin and sides of the  
head.

Berlepsch & Hellmayr failed to find any  
"type" of this bird in Neuchatel in 1905,  
but Hellmayr (Cat. Birds Amer., vii, 1934,  
445) writes "type in Neuchatel Museum."

***Tanagra analis* Tschudi =**

***Iridosornis analis analis* (Tschudi).**

*Archiv für Naturgeschichte*, x, (1), 1844, 287  
(Peru = Valley of Vitoc, Dept. Junin; Hell-  
mayr, Cat. Birds Amer., ix, 1936, 179, foot-  
note).

*Cotype*: U. S. Nat. Mus. 41919, unsexed,  
dismounted bird; Perou; wing 82, tail 69,  
culmen from base 13 mm.

Another cotype exists in the British Mu-  
seum (ex Sclater coll.) according to Sclater  
(Cat. Birds Brit. Mus., xi, 1886, p. 142).  
Hellmayr (Cat. Birds Amer., ix, 1936, p.  
179) states "type in Neuchatel Museum,"  
but in his earlier paper with Berlepsch,  
made no mention of this species among the  
Tschudi types still in that museum. Zimmer  
(*Field Mus. Nat. Hist.*, Zool. ser., xvii, 1920,  
443) writes that the "type may have come  
from near Lima since Tschudi says . . . the  
species was common in the fruit gardens of  
Lima, he did not find it further north or  
east . . ." However, Hellmayr (cit. supra)  
writes (from subsequent knowledge of the  
range of the bird) that Tschudi's statement  
is a mistake, and suggests the restricted  
type locality given above.

***Tanagra frugilegus* Tschudi =  
*Thraupis bonariensis darwinii*  
(Bonaparte).**

*Archiv für Naturgeschichte*, x, (1), 1844, 286  
(Peru = prob. fruit gardens of Lima).

*Cotype*: U. S. Nat. Mus. 41913, unsexed,  
(male by plumage); Peru (original label  
lost); wing 85, tail 73, culmen from base  
14 mm.

Another cotype went to the British Mu-  
seum (Cat. Birds Brit. Mus., xi, 1886,  
p. 165).

***Cissopis minor* Tschudi =  
*Cissopis leveriana leveriana* (Gmelin).**

Untersuchungen Fauna Peruana, Aves, 1846,  
p. 211 (wooded region of Peru; = Chacay-  
bamba?).

*Cotype*: U. S. Nat. Mus. 41914, unsexed,  
dismounted bird; Chacaybamba, Peru;  
4.8.39 (August 4 or April 8, 1839); wing  
112, tail 135, culmen from base 20 mm.

The data as to place and date are on the  
original field label in what is probably  
Tschudi's own caligraphy. The other speci-  
mens listed in this paper have only the  
original museum exhibition labels, which  
this bird has as well, and which merely read  
—"Perou. Voyage de M. Tschudi."

Hellmayr (Cat. Birds Amer., ix, 1936,  
439) states that the type (= another co-

type) is in Neuchatel Museum, but in 1905 he and Berlepsch failed to find it there.

***Arremon frontalis* Tschudi =**

***Atlapetes brunnei-nucha brunnei-nucha*  
(Lafresnaye).**

*Archiv für Naturgeschichte*, x, (1), 1844, 289  
(Peru = eastern wooded region between 8°  
and 9° lat. south and Jaen de Bracamoras,  
Peru).

*Cotype*: U. S. Nat. Mus. 41911, unsexed  
bird; original label lost; wing 79, tail 85,  
culmen from base 21 mm.

Although no type of this bird was found  
at Neuchatel in 1905 by Berlepsch &  
Hellmayr, the latter author (Cat. Birds  
Amer., xi, 1938, p. 413) states that a type  
is there. We therefore consider the present  
specimen a cotype.

Included with these types in the consign-  
ment from the Neuchatel Museum were four  
other Tschudi specimens which are not of  
type status. For the benefit of students  
wishing to unravel the synonymies of the  
species involved, they are listed below, to-

gether with references to the names under  
which Tschudi listed them.

***Ortygonax rytirhynchus rytirhynchus* (Vieil-  
lot).**

*Rallus caesi* (not of Spix) Tschudi, Unters.  
Fauna Peruana, 1844-46, p. 301.

One spec., U. S. Nat. Mus. 41934, (Perou).

***Columba plumbea delicata* Berlepsch & Stolz-  
mann.**

*Columba infuscata*, Tschudi, Unters. Fauna  
Peruana, 1844-46, p. 275.

One spec., U. S. Nat. Mus. 41929, (Perou).

***Thamnophilus melanocephalus* Sclater & Sal-  
vin.**

*Thamnophilus luctuosus* (not of Lichten-  
stein) Tschudi, *Archiv. für Naturgeschichte*,  
x, (1), 1844, p. 278.

One spec., U. S. Nat. Mus. 41910, (Perou).

***Molothrus bonariensis occidentalis* Berlepsch  
& Stolzmann.**

*Icterus brevirostris* (not of d'Orbigny and  
Lafresnaye) Tschudi, *Archiv. für Naturge-  
schichte*, x, (1), 1844, 292.

One spec., U. S. Nat. Mus. 41909, (Perou).





## 10.

A Revision of the Kingfishers, *Ceyx erithacus* and *rufidorsus*.

S. DILLON RIPLEY

These two species of kingfisher are important members of the Indo-Malayan avifauna. For many years their identification has proved a stumbling block and a very large amount of literature has collected around them. The most recent discussion of the problem, that of Chasen & Kloss (1929), has served to clear up many difficulties. I believe, however, that one or two interesting facts remain to be pointed out, and it is in an effort to do so that I have turned to these species in this paper.

Kingfishers in general tend to show a constancy of plumage pattern which is striking. Certain characteristic colors reappear again and again. Some colors, as brown and yellow, seem to be closely linked and substitute for each other with great regularity. Plumage patterns are nearly uniform throughout the family. In the case of these two species of *Ceyx*, the color and size resemblances are so particularly close that the conclusion that these birds are very nearly related seems inescapable.

The next nearest relation of these two species is *Ceyx melanurus* with three races from the Philippines.

I am much indebted to Mr. J. L. Peters for reading over this manuscript as well as to the authorities of the United States National Museum, the Academy of Natural Sciences of Philadelphia and the American Museum of Natural History for the loan of specimens. In the following discussion all measurements are in millimetres, the wing pressed flat against the ruler, and the bill measured from the distal end of the external naris to the terminal point of the maxilla.

For easy identification of these two species, it might be well to insert here a key by which identification can be made.

- A. Upper parts rufous with a lilac wash.
  - a. Forehead with a dark blue-black spot . . . *C. erithacus*.
  - b. Forehead spot absent . . . *C. rufidorsus*.
  - a'. A patch of ultramarine in the supraocular region . . . *C. erithacus*.
  - b'. Supraocular patch lacking . . . *C. rufidorsus*.

- a". Scapulars black with an ultramarine wash . . . *C. erithacus*.
- b". Scapulars rufous with a lilac wash . . . *C. rufidorsus*.
- a' ". Wing coverts black tipped with ultramarine . . . *C. erithacus*.
- b' ". Wing coverts rufous tipped with lilac . . . *C. rufidorsus*.

*Ceyx erithacus erithacus* (Linnaeus).

*Alcedo erithaca* Linnaeus, Sys. Nat. 10, T. p. 115, 1758.

*Description*: For the adult bird see Sharpe (1892, p. 175). The rufous on the bend of the wing often extends to the lesser wing coverts.

Juvenal birds are distinguished from adults by several characteristic features. The bill is rather short and pale, often dusky at the base. On the upper surface the plumage is the same as the adult, but the scapulars tend to be tipped rather than washed with ultramarine. Instead of being washed with lilac, the feathers of the lower back sometimes are tinted with cobalt. The tail is often, but not invariably, tipped with black. Below, juvenal and immature birds show a very characteristic plumage. The throat is pure white not tinted with yellow. The lower cheeks, flanks, thighs, under tail coverts, and a band across the breast and upper abdomen are rufous, sometimes with an orange tint.

*Measurements*: Wing, ♂ 53–58.5 (55.8), ♀ 55–60 (56.8). Tail, ♂ 20–23.5 (22.6), ♀ 2.15–24.5 (23.1). Wing-tail index 38–42%. Bill, from naris, ♂ and ♀, 25–28.2 (27.2).

*Range*: Ceylon through the lowland coastal parts of India to Nepal, Assam, Burma, *vide* Stuart Baker (1927), the Malay Peninsula, Siam, Indo-China, southern China, Hainan, Andaman Ids, small islands in the Straits of Malacca and off the Malay Peninsula, coast of Sumatra.

*Specimens Examined*: Sixteen.

*Discussion*: This form is well established in continental Asia but only sparingly distributed among the islands. Such a distribution indicates a later origin than that of *rufidorsus* which has extended into the

Greater and Lesser Sunda area. The latter having become established in the Greater Sundas and adjacent islands, there has been a secondary infiltration perhaps in two waves by *erithacus*, which has succeeded in colonizing a few of the small islands not already reached by *rufidorsus* (Nicobars, Nias) and in competing with the latter species in the larger continental areas (Malay Peninsula, Borneo).

From the evidence afforded by specimens, Sumatra seems to be primarily the home of *rufidorsus*. I have examined the type of *Ceyx enopopygius* (Oberholser, 1912) and concur with Chasen & Kloss (1929) in their belief that it is an unusually bright immature specimen. The measurements of this specimen (wing 57.5, tail 23.5, bill 27.7) are not different from normal *erithacus*. The only other examples of *erithacus* from Sumatra are two males listed in Laubmann (1925). These three records are from coastal localities and this coupled with Robinson & Kloss' (1922) record of this species as being a bird commonly killed at one of the lighthouses in Malacca Strait leads me to suspect that the Sumatra records are accidental. These birds in contrast to *Ceyx rufidorsus* (Robinson, 1917) are subject to erratic local movements which result in isolated records appearing all over the islands of Malacca Strait and the adjacent Sumatran coast. This is a subject which should be studied more carefully. It is possible that some physiological dispersal mechanism is at work here which may be akin to migration.

***Ceyx erithacus macrocarus* Oberholser.**

*Ceyx erithacus macrocarus* Oberholser, *Bull.* 98, U. S. Nat. Mus., 23, 1917.

**Description:** Differs from *erithacus* by being larger. The forehead spot is smaller in two examples.

A nestling, A.M.N.H. 637008, is colored as the adult except for the reduction of the ultramarine wash on the scapulars back and median wing coverts to a series of spots. The shaft and the terminal part of the tail are black. Below the bird is similar to young of *erithacus*. This specimen was collected Oct. 4, 1905.

**Measurements:** Wing, ♂ 58–60.3 (59.4), ♀ 61. Tail, ♂ 23.–24 (23.4), ♀ 24.5. Wing-tail index 39–40. Bill, ♂ and ♀ 30–31 (30.4).

**Range:** Great Nicobar, Nicobar Ids.

**Specimens Examined:** Five.

**Discussion:** The most significant character of this race is its larger size, especially in bill measurements. It is interesting that the Andamans seem to be populated by typical *erithacus*. This is in contrast to the usual case in which Andaman and Nicobar populations tend to be identical. A single male from South Andaman (A.M.N.H.

637011) is characteristically of the smaller subspecies. This particular specimen is notable for a very heavy blue forehead spot which extends back broadly onto the crown.

In order to check on the above measurements, I have estimated the probability of these two populations being identical by use of the formula of *T* for deviations from the mean in small samples as discussed by Simpson & Roe (1939). This formula allows a very critical estimation when, as in this case, the combined samples of adult specimens are less than fifteen. By using the formula on the wing, tail, and bill measurements, *T* proves to be very significant for the bill (6.0), significant for the wing (3.1) and insignificant for the tail (1.5). Thus even on the basis of the bill alone, *macrocarus* is a justifiable race.

***Ceyx erithacus motleyi* Chasen & Kloss.**

*Ceyx erithacus motleyi*, Chasen & Kloss, *Festsch. für E. Hartert, Journ. f. Ornith.*, p. 106, 1929.

**Description:** This and the following two races differ from *erithacus* and *macrocarus* by having the rufous tinted with lilac of the pileum and nape extending down on the back and continuous with the lower back and rump. The rest of the plumage, however, is similar to the typical subspecies.

The immature plumage differs from the adult as in *erithacus*.

**Measurements:** Wing, ♂ 57.5–60.5 (59.5). Tail, ♂ 22–24 (22.8). Wing-tail index 36–39. Bill, ♂ 28.5–30 (29.1).

**Range:** Borneo, Banguey Is, Labuan (?).

**Specimens Examined:** Five.

**Discussion:** The confusion resulting over the description of *Ceyx dillwynni* and *sharpei* from Borneo was finally resolved by Chasen & Kloss (1929). I believe, however, that they were mistaken in assuming Sharpe's plate of *dillwynni* (1868-71) to be a representation of an immature specimen of *rufidorsus*. I have before me two male adult specimens (M.C.Z. 197135, 197136) which correspond very closely to Sharpe's plate. I believe that they are hybrids between *rufidorsus* and *motleyi*. From a careful examination of the specimens it is difficult to escape the conclusion that where *erithacus* overlaps into the range of *rufidorsus*, hybridization has occurred. Indeed Sharpe had apparently already begun to suspect this by the time that he was working on the Catalogue of the Birds in the British Museum. In that volume (1892) he transfers his original description of *dillwynni* to a description of what is now *motleyi* and lists several dubious specimens which he remarks may be "in changing plumage . . . or are hybrids." A description of some of these specimens may be appropriate at this point.

(1). M.C.Z. 197135, ♂, ad. Kalabakang R., Borneo, coll. July 7, 1937. H. G. Deignan. Above this specimen is similar to typical *motleyi*, but the forehead spot is very much reduced as is also the supraocular patch of ultramarine. The scapulars are washed with ultramarine, but tipped with pale lilac. The lesser and median wing coverts are strongly rufous (more so than in Sharpe's plate). The distal outer margins of the secondaries as well as the inner margins are edged with rufous. Below the bird is similar to the adult of either *rufidorsus* or *erithacus*.

(2). M.C.Z. 197136, ♂, ad. Kalabakang R., Borneo, July 14, 1937. H. G. Deignan. Above this specimen lacks any hint of forehead spot and again the supraocular patch of ultramarine is nearly gone. The scapulars are as in *motleyi*, but some of the upper median wing coverts are rufous and the greater wing coverts and outer margins of the secondaries are irregularly tipped with rufous.

(3). M.C.Z. 197134, ♂, ad. Sandakan, Borneo, June 18, 1937. H. G. Deignan. Above this specimen is uniformly rufous with a lilac wash. There is no trace of either forehead or supraocular spot. The scapulars present a curious violet tone from the mingling of ultramarine and lilac washes. The lesser median wing coverts are rufous. The greater wing coverts are black with a bluish-lilac subterminal wash and rufous edgings. This bird stands almost exactly in an intermediate position between *motleyi* and *rufidorsus*.

(4). M.C.Z. 69608, ad. Linibang, Sarawak, Borneo, no date. Above this bird has a forehead spot and supraocular spot. The scapulars are, however, predominately rufous-lilac. The lesser and median wing coverts are rufous, the greater strongly tipped with ultramarine.

(5). M.C.Z. 69610, ad. Borneo, 1915. H. W. Smith. Above this bird is similar to *rufidorsus*. However, it is an adult specimen and so should not have curious patchy blackish and ultramarine tinted scapulars. The wing coverts are similar to *rufidorsus* except that there is a hint of ultramarine on the tips of some of the greater one.

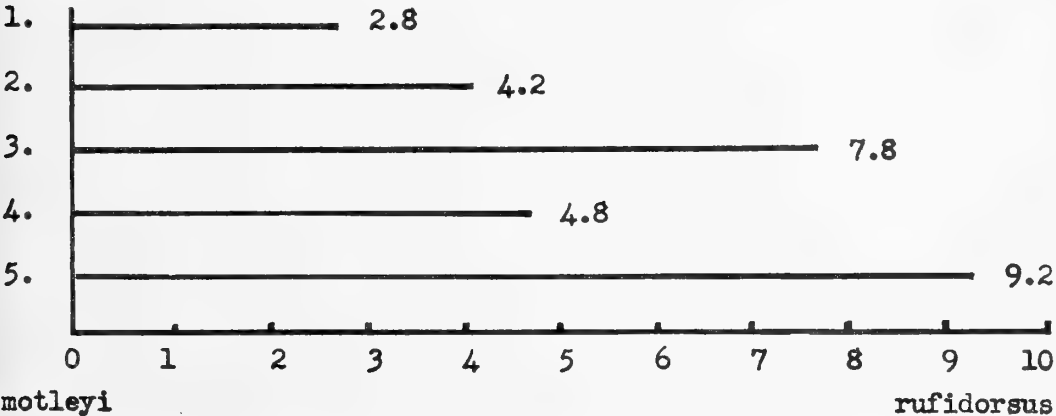
cept that there is a hint of ultramarine on the tips of some of the greater one.

(6). M.C.Z. 69609, o im., Kuala Treban, Sarawak, Borneo, Feb. 28, 1918. An immature hybrid is of interest. Above this specimen shows a prominent forehead spot and the merest trace (two feather tips) of a supraocular patch. The scapulars are black with a few faint tips of ultramarine. The lesser and median wing coverts are largely rufous, the greater are black, washed with ultramarine and with faint rufous edgings. Below this bird is typically immature, having a white throat and strongly rufous cheeks, flanks, and breast band.

The above specimens represent almost a complete transition from *erithacus motleyi* to *rufidorsus rufidorsus*. Each bird represents a greater or less blending of the distinctive characters of the two species. Here indeed is an interesting example of two closely related forms of kingfisher which do not quite satisfy any of the concepts of taxonomy or speciation. On the one hand the color of the back is so different that many taxonomists would consider these birds to belong to two species. Others might lump them, if it were not for the over-lapping of their ranges. From the speciation point of view they do not conform either to a Super-species or to a *rassenkreis*. And yet the birds would satisfy any geneticist as to their close ancestry by their apparent readiness to hybridize.

Shown on a linear scale, the characters of these hybrids indicate quite clearly their intermediate position. Letting certain characters equal certain numbers we arrive at an arbitrary scale as follows:

	<i>erithacus motleyi</i>	<i>rufidorsus rufidorsus</i>
Forehead spot	present—0	absent—10
Supraocular spot	present—0	absent—10
Scapulars	blue—0	rufous lilac—10
Lesser & median wingcoverts	black—0	rufous—10
Greater wing coverts	black—0	rufous—10



Text-fig. 1. The numbers on the left are those of the individual specimens. The base line represents the scale from *motleyi* to *rufidorsus*. At the end of each specimen's line is the figure representing the sum of its characters.

By adding up each specimen's score and dividing by five we arrive at the following:

The original description of *Ceyx dillwyni* Sharpe (1868) would have sufficed for the local race of *erithacus*, if it had not been for the fact that not only did Sharpe not mention a supraocular patch as occurring on his type, but Salvadori (1869) specifically says that it did not have one. I cannot find a single undoubted specimen of the species *erithacus* which does not possess this spot. Any specimen, therefore, coming from Borneo or Sumatra or the Malay Peninsula (as will be seen later) which is an adult but does not possess either the forehead spot or supraocular patch, and yet which has ultramarine on scapulars or wing coverts must be considered to be potentially a hybrid.

### *Ceyx erithacus captus* Ripley.

*Ceyx erithacus captus* Ripley, *Proc. New Eng. Zool. Club*, XIX, 15, Dec. 29, 1941.

*Description*: This race differs from *motleyi* by its longer bill and slightly larger size, and by reduction of the forehead spot which is lacking in one specimen. This last character was not mentioned in the original description due to the fact that the question of the hybrid population of *motleyi* has not been elucidated.

From *erithacus* this race differs as *motleyi*.

I have seen no immature specimens.

*Measurements*: Wing, ♂ 59.5–62.5 (60.8). Tail, ♂ 23–24 (25.6). Wing-tail index 39–40. Bill 32–33.5 (32.6).

*Range*: Nias I. West Sumatra.

*Specimens Examined*: Three.

*Discussion*: It is interesting to note that *captus*, as *macrocarus*, differs from its nearest relative by size. In this case it is the bill which is notably larger. Like *macrocarus*, also, the forehead spot and the supraocular patch are much reduced.

### *Ceyx erithacus vorgasi* Manuel.

*Ceyx erithacus vorgasi* Manuel, *Phil. Journ. Science*, 69, No. 4, 383, Aug., 1939.

*Description*: Differs from *motleyi*, which it otherwise closely resembles, by the reduction of the lilac wash on the upper surface. In the specimen examined this wash occurs only in a supraorbital stripe ending in an ultramarine supraocular patch, and on the lower back, two areas where the color is most highly concentrated in *motleyi*. The ultramarine wash on the scapulars also is reduced to the tips of one or two feathers. The specimen examined, though otherwise in adult plumage, has a black shaft and a black stripe along the middle of the terminal half of the tail feathers.

*Measurements* (one female): Wing 56.5. Tail 24. Wing-tail index 42. Bill 28.5.

*Range*: Mindoro I., Philippine Islands.

*Discussion*: The existence of this population of *Ceyx erithacus* was only discovered in 1939 by Manuel who noticed that two specimens of *Ceyx* had the blue supraocular patch not found in *rufidorsus*. It is worth noting that *Ceyx melanurus* behaves in a strictly representative way in the Philippines with *rufidorsus*, while *erithacus* has incurred on the range of *rufidorsus* on Mindoro.

### *Ceyx rufidorsus rufidorsus* Strickland.

*Ceyx rufidorsus* Strickland, *Proc. Zool. Soc.*, p. 99, 1846.

*Ceyx innominatus* Salvadori, *Atti R. Accad. Sci. Torino*, IV, p. 465, 1869.

*Description*: Above, rufous washed with lilac, scapulars and wing coverts as the back, primaries black, the first edged with rufous, secondaries black edged with rufous. Ordinarily this species lacks a dark forehead spot (three times present in 25 examples) and an ultramarine supraocular patch (twice present in 25 examples). Below the throat is white, the rest of the underparts being rich yellow.

Immature birds differ from the adult by having less of the bright lilac wash on the rufous upper parts. A nestling (A.M.N.H. 637014) from Gunong Tahan, Pahang, Malay Penin., collected in November, has black scapulars tinted with rufous and with one or two faint spots of ultramarine. The wing coverts tend to have rather more black than the adult. The tail is entirely rufous. Below the throat and belly are white, the cheeks, flanks, and a band across the abdomen rufous.

An immature male from East Java (A.M.N.H. 637034) collected in August, has completely rufous scapulars. This bird is one of the specimens which has an ultramarine spot above the ear. Below it agrees with the other specimens.

An immature female from Borneo (A.M.N.H. 637055) collected in September, has blackish scapulars overlaid with rufous and a black-tipped tail.

*Measurements* (adults): Wing, ♂ 56.5–60.5 (58.2), ♀ 59.5–60.5 (60). Tail, ♂ 22.7–25 (23.7), ♀ 24–24.7 (24.2). Wing-tail index 39–41. Bill, from naris, ♂ and ♀, 27–32 (28).

*Range*: Malay Peninsula, Rhio and Lingga Islands, Banka, Billiton, Sumatra, Siberut, Sipora, Java, Bali, Lombok, Sumbawa, Flores, Kangean, Bawean, Borneo, North Natuna, Anamba Ids, and Philippines, Palawan, Balabac, Mindoro, Tawitawi, Bongao, Calamianes.

*Specimens Examined*: Twenty-one.

*Discussion*: Several specimens from the Malay Peninsula and Sumatra have been noted which appear to be hybrids.

(1). An adult female (A.M.N.H. 637027) from the Deli district of Sumatra, Van Heyst coll., has a prominent forehead spot

and an infusion of ultramarine in the supra-ocular area. The scapulars, lesser and median wing coverts are mixed with black and ultramarine.

(2). Another adult female (M.C.Z. 17707) from Benkoolen, Sumatra, has a prominent forehead spot and blackish scapulars and wing coverts irregularly spotted with traces of ultramarine.

(3). A juvenal male (U.S.N.M. 180199) from Kateman River, E. Sumatra, collected in August, has the forehead spot and black tipped with ultramarine scapulars of *erithacus*, but it lacks the supraocular patch. The terminal half of the tail along the shaft of the feathers is black.

(4). An immature specimen from Great Karimon Id., E. Sumatra, (U.S.N.M. 180198) collected in May, has a black forehead patch and mixed scapulars, black and rufous, with lilac and ultramarine spots.

(5). A male molting into adult plumage (A.M.N.H. 637012) from western Pahang, Malay Peninsula, collected in January, has the blue forehead spot and supraocular patch of *erithacus*. However, the wing coverts, as in some of the Bornean hybrids, are mainly rufous.

These specimens indicate clearly that wherever the range of these two species overlap, there is a pronounced tendency to hybridization. From them it is clear that any specimen from Sumatra, the Malay Peninsula or Borneo, which seems to be adult but has either of the following combinations, must be suspect.

Hybrid Type A: Forehead spot and supra-ocular patch present, but scapulars and wing coverts largely rufous.

Hybrid Type B: Forehead spot and supra-ocular patch absent, but scapulars and wing coverts largely black with an ultramarine wash.

Specimens from Java tend to be slightly smaller, but tests for the significance of these data by the formula of *T*, show that the differences are not valid and the name *innominatus* cannot be upheld.

### *Ceyx rufidorsus jungei* ssp. nov.

Type: M.C.Z. no. 178157, ♂ ad., collected by E. Jacobson and W. C. van Heurn, July 28, 1913, Ajer Dingin, Simalur I.

Diagnosis: From *C. r. rufidorsus* this race differs by its larger size.

Measurements (of type): Wing 62, tail 26, bill 31.5; (of series): Wing, ♂ 62–64.5 (63.2), ♀ 62.5–63.5 (63). Tail, ♀ 25–26 (25.5), ♂ 25.5–26.5 (26). Wing-tail index 39–42. Bill, ♂ and ♀, 30.5–32 (31.3).

Range: Simalur and Batoe Ids, Tanah Massa and Tanah Bala.

Specimens Examined: Seven.

Discussion: This race is decidedly larger than *rufidorsus* from the rest of the range. It is interesting to note that the bill measurements, though averaging larger, are not

significantly so when the probability is computed by standard deviation. Birds from Siberut and Sipora, as listed by Chasen & Kloss (1926), agree in size with typical *rufidorsus*. Here again, as in the two races of *Ceyx erithacus* on small islands north and west of Sumatra, this population of kingfishers differs from its nearest relatives by larger size. This race is named in honor of Dr. G. C. A. Junge of the Leiden Museum who has always been interested in East Indian birds.

### CONCLUSION.

*Ceyx erithacus* and *rufidorsus* are closely allied species and might be considered conspecific were it not for the fact that their ranges are overlapping. In the Malay Peninsula, Sumatra and Borneo where this occurs, specimens were examined which show hybrid characters indicating that the earlier confusion in the nomenclature was probably due to this phenomenon. *Ceyx rufidorsus* is considered to be the older species due to its more extensive range.

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## 11.

On the Reproduction of *Gobiosoma robustum* Ginsburg.

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(Plates I &amp; II; Text-figure 1).

## INTRODUCTION.

The small and active goby, *Gobiosoma robustum* Ginsburg, inhabits a wide range of territory on the west coast of Florida near the field station of the New York Aquarium located on Palmetto Key. There appears to be nothing whatever in the literature on the habits or behavior of this common fish. The observations and data presented herewith were gathered incidental to studies of the life histories of other species in this region (see Breder 1939a and b, 1941a and b). Mr. M. B. Bishop of Yale University, Mr. L. A. Krumholz of the University of Illinois and Mr. B. Dontzin of Cornell University all rendered valued assistance in connection with this study.

This species, differentiated from related forms by Ginsburg (1933), represents the only member of the genus found occurring near the laboratory. Here it is abundant and may be taken in numbers among the mangrove roots and on open sandy beaches. Dredging brought it up from depths as great as twenty feet, which represents the deepest of this shallow bay in the vicinity of the laboratory. It was taken in such equipment over all of the various types of bottom, such as grassy places, sponge beds, scallop beds, sand bars and even over soft spots of flocculent mud.

The individuals of this form are exceedingly variable. Fowler (1941) figures six patterns represented in his material. Some of the pattern differences are referable to sex but they are so overlaid with individual vagaries that exact description becomes difficult. Nevertheless with a little experience it is possible to sex individuals with reasonable accuracy.

Shropshire (1932) figures the young of a *Gobiosoma* under the name *Gobiosoma molesum*. It is impossible to tell just which form, under present terminology, he had. *G. moles-*

*tum* Girard is now a synonym of *G. bosci* (Lacépède) but as Shropshire thought his material was not the latter it is possible that he was actually dealing with *G. robustum* as here understood.

There is no confusion about the identity of the present material as the fish were taken guarding their eggs and furthermore all other specimens in our collections are referable to this one species, and it is the only form definitely known to be living in the vicinity. Dr. I. Ginsburg, the describer of *G. robustum*, was good enough to check over this material and compare it with his large series of both species.

## NESTING AND NESTING SITES.

*Gobiosoma robustum* may be found with its eggs from March to June, at least. At first this finding led to the assumption in the field that there were more than one species included. However, since a critical study of the incubating fishes shows them to be referable to a single species, it follows that this form has a long spawning period which reaches from the coldest to the warmest period of the year. It may well be that actually spawning is in progress at all times, which, if true would account for the relatively small number of nests encountered at any one time, compared with the abundance of individuals in the region.

The nests so far located have all been in shells or sponges. Usually the eggs are found hanging from the underside of some surface, but are not necessarily in such a position. Plate I, Figure 1, shows the two valves of a *Pecten* shell with the eggs attached to what had been the lower shell and the guarding male with them. This fish continued caring for the eggs with the shell in its open position.

## COURTSHIP AND PARENTAL CARE.

Apparently only the males guard the eggs, as females have never been found in

the vicinity of nests. The males fan and work over the eggs in a manner reminiscent of a fresh water darter. Beyond this nothing was noted in the matter of specialized behavior. Although the males would attack small animals, such as other gobies, the slightest disturbance of a larger sort would usually cause them to retire. They would return as soon as the disturbance subsided.

Although we were not successful in having this species spawn in aquaria, several males established themselves in sheltered places which they would defend against the intrusion of their tank mates. From such locations they would sally forth to court nearby females. This was done with much spreading of the fins, especially the dorsal, accompanied by short darts near or at the female. This was usually carried on until she retreated. The coloration of the male at these times became intense and dark, nearly black, in most cases; most notably so on the widely extended first dorsal fin.

The largest male seen was 34 mm. in standard length. This is the fish shown in Plate I. The smallest mature and ripe male seen was 16.5 mm. Ripe females examined ranged from 16.5 to 21.5 mm. Apparently the males not only reach a larger size but average somewhat larger than the females as well. Smaller individuals grading down to those of a few millimeters are present both summer and winter, again indicating a long if not continuous reproductive season.

#### THE EGGS.

The elongate eggs are attached by one end to a matted base of adhesive threads. They are evenly elliptical but there is an apparent seasonal difference in their proportions. Those taken in March average rather differently than those taken in June according to the following schedule, measured on living eggs and given in mm.

No. of eggs	Months	Average	Length	Minimum	Average	Width	Minimum
			Maximum			Maximum	
8	March	1.62—	1.70	1.55	0.62—	0.70	0.60
2	June	1.35	1.40	1.30	0.50	0.50	0.50
10	All	1.57	1.70	1.30	0.60	0.70	0.50

These differences would seem to be referable to seasonal effects, probably chiefly temperature, controlling the speed of development of the ovarian eggs. Another possible interpretation is that this is an expression of incipient speciation, starting first with a prolonged spawning season finally reaching over the extremes of summer and winter temperatures. Those fish most responsive to temperature variations, at either end of the long season, might be beginning to show slight differences in reproductive items, in this case egg size, finally leading to the establishment of two fairly distinct forms with, perhaps, intermediates

dropping out. In this connection the differences in the spawning times of *Opsanus tau* and *Opsanus beta* discussed by Breder (1941a) is suggestive.

The winter eggs are shown in six stages of development in Text-fig. 1. When first found they appeared as in "A," March 14, 3:45 p.m. The yolk and germinal parts are opaque and slightly yellowish. The elliptical envelope is clear and without markings. Attachment is at one end by means of a tangled mass of adhesive strands. The nature of this material is better shown in the photographs of Pl. II. In many of the eggs the yolk was nearer to the upper tip than to the center. Numerous exceedingly small droplets, hardly visible at lower powers, were scattered over the surface of the yolk as indicated in the sketches. Twenty-two and a quarter hours later the eggs appeared as shown in Text-fig. 1, "B." At this stage the swelling of the large head was especially prominent. In an additional twenty-six and a quarter hours the embryo was well formed and appeared as in Text-fig. 1, "C." Both yolk and embryo presented an opaque appearance. After twenty and one-quarter hours more the embryo had reached the proportions shown in Text-fig. 1, "D." At no time was there a sufficient transparency to evidence much of the internal structure. The side view seen in Text-fig. 1, "E," when the egg was twenty-one hours more advanced, shows some of the vertebral fragmentations. By the time an additional twenty-seven and one-half hours had passed the heart was evident and beating slowly and the tail gave spasmodic twitches.

These figures cover a period of 117½ hours during which time the temperature in the incubating dishes ranged from 15.5 to 18.5° C. It was noted that some of the eggs were not as advanced as others, indicating at least more than one spawning. These fig-

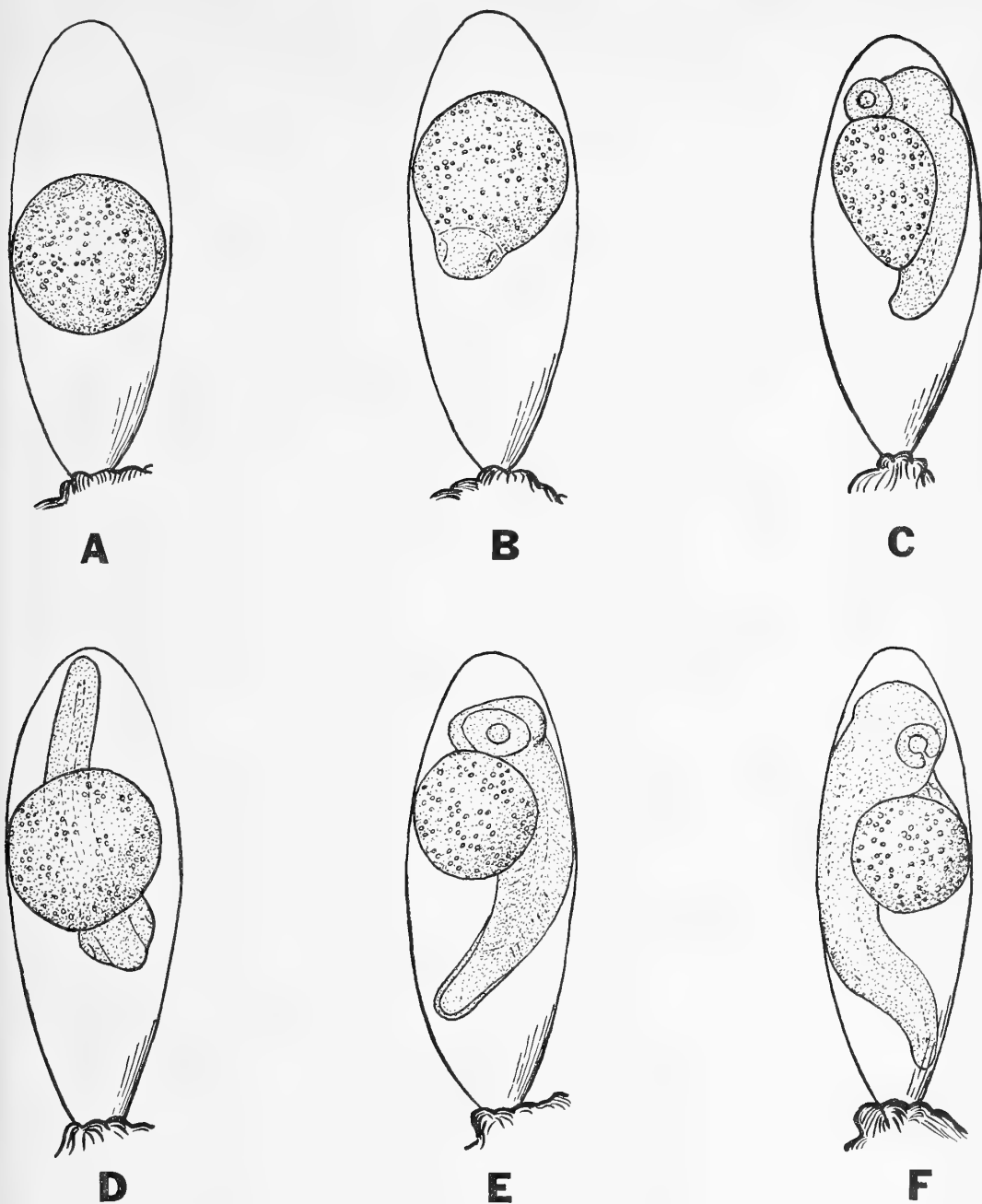
ures are based on the youngest eggs. By the time the last stage was reached they were practically equal, so far as gross examination was concerned. Plate II, Figures 2 and 3, give some indication of the differences in the extent of advancement of the eggs, especially if compared with the sketches of Text-fig. 1.

By March 24 all the eggs were dead, presumably due to extreme temperature fluctuations in the laboratory.

#### DISCUSSION.

The development of the eggs of *Gobiosoma bosci* (Lacépède) has been described in de-





Text-fig. 1. Stages in the development of the eggs of *Gobiosoma robustum*. Camera lucida sketches of living material. A. An early egg as found in nest. B.  $22\frac{1}{4}$  hours older than "A," with cephalization well advanced. C.  $48\frac{1}{2}$  hours older than "A," with the tail reaching well beyond the yolk. D.  $68\frac{3}{4}$  hours older than "A." E.  $89\frac{3}{4}$  hours older than "A." F.  $117\frac{1}{4}$  hours older than "A," with the heart beating and the embryo showing activity.

tail by Kuntz (1916) and discussed at length by Hildebrand & Cable (1938). A comparison of the present notes on *G. robustum* with these papers shows the details to be quite similar, as would be expected on two

such close species. The eggs of the latter average slightly longer and wider than those of *G. bosci*, as is indicated by the following tabulation of ranges in size, given in mm.

Species		Long Diameter	Short Diameter
<i>G. bosci</i>		1.15-1.37	0.57-0.59
<i>G. robustum</i>	All	1.30-1.70	0.50-0.70
	Summer	1.35-1.40	0.50-0.50
	Winter	1.62-1.70	0.62-0.70

It will be noted that the summer measurements are closer to those of *G. bosci* than those of the winter. The *G. bosci* material was likewise taken in summer. Hildebrand & Cable (1938) found young from May to December on the North Carolina coast, indicating a long season for this species also but with a winter interruption which is probably more a matter of geography and temperature than a specific difference. This strengthens the view that spawning may take place throughout the year on the much warmer Florida west coast. They found the young sometimes in the surface tows but more frequently in the bottom tows, indicating that they do not spend much time as plankton, an item also noted in the *G. robustum* material. Dip nets have found them in very small sizes clinging to floating drift, such as bits of plant stems, and it seems that most specimens taken in surface tows come from such locations, as even in very small sizes they sink rapidly and are not given to much active swimming other than short darts between supporting objects. Apparently sustained swimming is a considerable effort for these fishes.

The eggs of *Gobiosoma* and a number of related genera are remarkably similar as are their reproductive habits and it would be pointless at this place to discuss the perhaps minor differences of uncertain clarity until much more is known in greater detail about more of the numerous species.

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#### EXPLANATION OF THE PLATES.

##### PLATE I.

Fig. 1. Male *Gobiosoma robustum* guarding nest in an opened scallop shell.

##### PLATE II.

Fig. 2. Photomicrograph of the living eggs in about the stage shown in Text-figure 1, A.

Fig. 3. Photomicrograph of the living eggs in about the stage of Text-figure 1, E.



FIG. 1.

ON THE REPRODUCTION OF *GOBIOSOMA ROBUSTUM* GINSBURG.



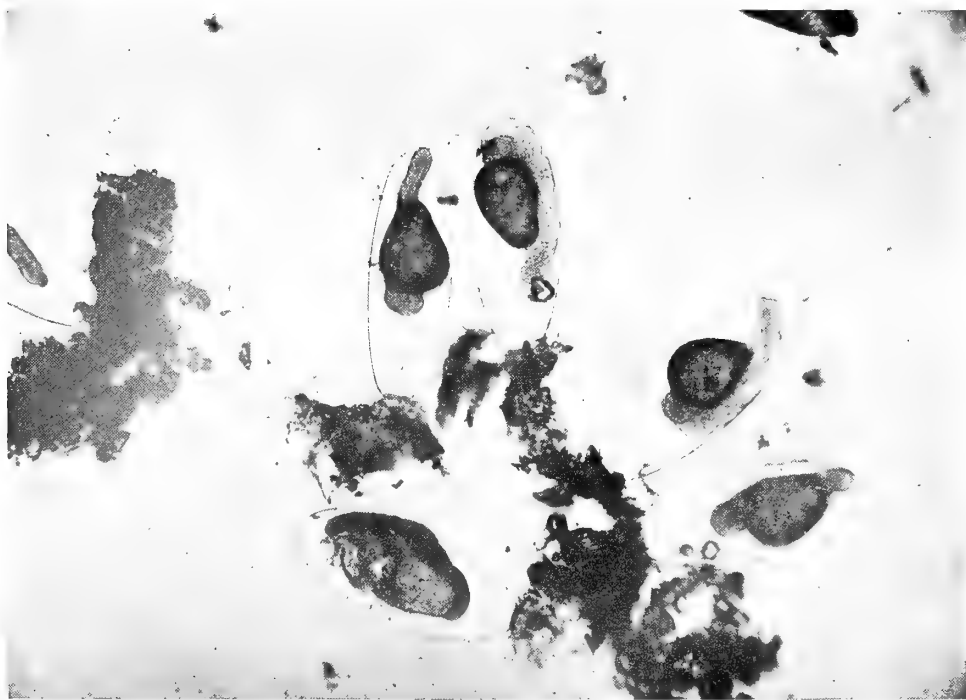
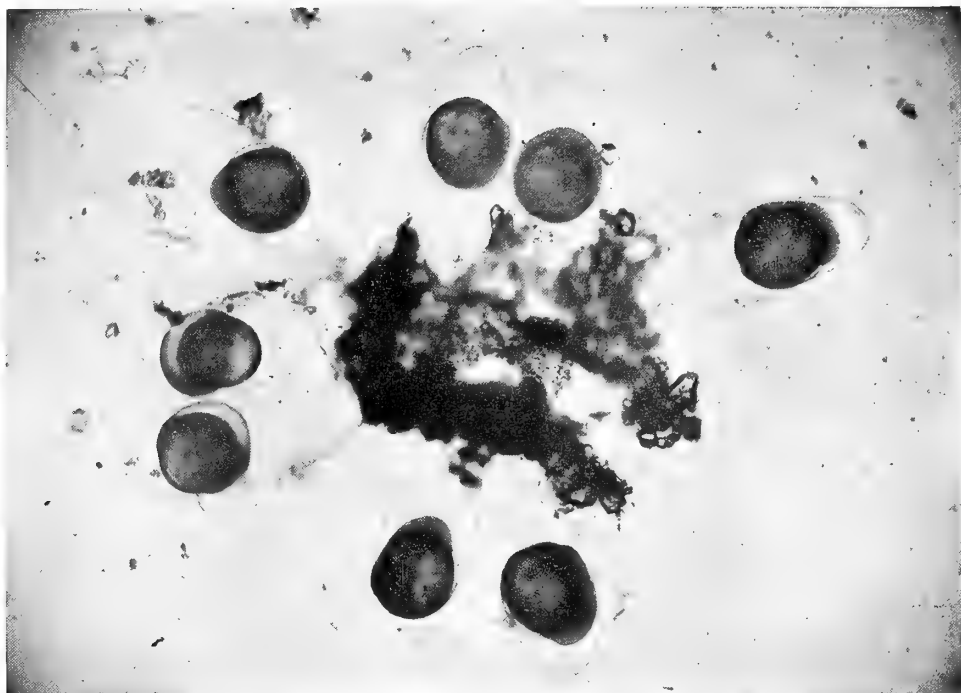


FIG. 2.

ON THE REPRODUCTION OF *GOBIOSOMA ROBUSTUM* GINSBURG.



## 12.

***Trichodina spheroidesi* and *Trichodina halli* spp. nov. Parasitic  
on the Gills and Skin of Marine Fishes, with Special  
Reference to the Life-history of *T. spheroidesi*.**

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&amp;

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Plates I-III; Text-figures 1-4.

## INTRODUCTION.

Marine members of the family Urceolariidae have been described from several species of invertebrates and vertebrates. Among those parasitizing fish are the following: *Trichodina scorpaena* Robin (1879) from the gills of *Scorpaena* and *Trigla*; *T. labrorum* Chatton (1910) from two species of *Symphodus*; and, *T. fariai* da Cunha & Pinto (1928) from the intestine of the smooth puffer, *Spheroides testudineus*. Fantham (1918, 1919, 1924, 1930) reported *Trichodina* from several fishes of which the following were definitely identified as new in his 1930 paper: *Trichodina clini* from *Clinus taures*, *C. superciliosus*, *C. capensis*, *C. cottoides*, *C. anguillaris*, *Pristopoma bennettii* and *Box salpa*; *T. blenni* from *Blenius cornutus*, *T. mugilis* from *Mugil capito* and *T. chelidonichthys* from *Chelidonichthys cupensis*.

Because of insufficient information on many of the above forms, it was extremely difficult to arrive at a definite conclusion as to the validity of these species. In the present studies, the writers encountered two forms of *Trichodina* parasitic on the gills and skin of puffers (*Spheroides maculatus*) and other marine fishes from the New York and New Jersey coast. These peritrich ciliates are easily distinguished from one another on absolute size and other characters. The one, a smaller and more abundant form, is designated *Trichodina spheroidesi*. The other, larger in all respects and less frequently encountered, is called *Trichodina halli*. This species can easily be distinguished from other *Trichodina* infesting

marine fishes on the basis of body size and size and relationships of the organelles (see Table).

## MATERIAL AND METHODS.

Between the months of June and the early part of October, from 1938 to 1940, about three hundred of the puffers taken in pound nets in Sandy Hook Bay were examined for *Trichodina*. Two hundred and forty-eight, or 82%, of the fish were found parasitized, the intensity varying considerably.

A number of gill samples were fixed in Schaudinn's fluid without acetic acid, and others were fixed in 10% neutral formalin. The material was stained with Heidenhain's iron-hematoxylin and Mallory's triple stain. A few samples of those treated by the former method were counterstained with "light green." Only the Schaudinn-fixed specimens were found suitable for cytological studies. Studies on the adhesive disc and denticulate ring were made from both the Schaudinn and formalin fixed material.

A combination of the Klein's (1926) silver impregnation and the De Fano's reduction techniques was used to determine the ciliary pattern. Especially good results for such studies were obtained with material fixed with formalin. The samples were washed in five changes of distilled water, impregnated with a 5% solution of silver nitrate for a period of eight to twelve hours, and placed in darkness. Following the removal of excess silver nitrate solution the material was reduced in De Fano's solution. The films were toned in a 3% solution of sodium hydrosulphite and sodium anthraquinone sulphonate (25:1). This method,

although not delicate enough to give a distinct silver line system, nevertheless effectively demonstrated the ciliary pattern, including the basal granules.

Measurements were taken of the height, the diameter of the organism, the diameter of the adhesive disc and of the denticulate ring. A count was made of the hook number on all mounted organisms.

#### HOST-PARASITE RELATIONSHIPS.

A variety of fishes indigent to the Sandy Hook area were found to harbor *Trichodina* (Nigrelli, 1940). The infestation on any one host species was never found as consistently or as intense as on the puffers. Insofar as could be determined, trichodiniasis among puffers was limited to fish on the New York and New Jersey coast, for examination of this species from the coast of Massachusetts during part of the period of this investigation did not reveal infection.

A few migratory *Trichodina* were found moving about on the body surface of puffers. However, the heaviest infestation was always on the gills. This may be attributed to the small opercular opening which encourages the concentration of these ciliates in the gill chamber.

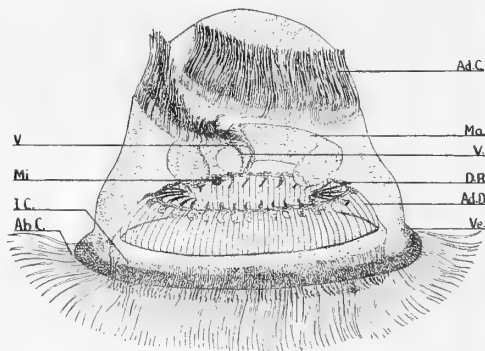
The presence of red blood cells in food vacuoles of the parasites show that they are capable of considerable tissue destruction. This is indicated further by the fact that in exceptionally heavy infestation the gill epithelium was completely destroyed, leaving large denuded areas among the filaments. Such a condition results in the death of the host.

#### *Trichodina spheroidesi* sp. nov.

(Text-fig. 1).

**Description:** Organisms turban shaped. Diameter ranges from 17–54  $\mu$ ; height from 12–42  $\mu$ . Two parallel rows of adoral, long, flexible, closely set, cilia present; cilia begin a short distance from the base of the peduncle, make one and a quarter clockwise, spiral turns and terminate in the vestibulum just above the mid-sectional plane of the oral surface; cilia, shortened noticeably at a point near the entrance of the vestibulum, spirals twice along the wall of the vestibulum and at the lower end are twisted together; direction of this spiral, when viewed from the end of the vestibulum outward, also clockwise. Aboral region with two rings of cilia; one ring, fused to form a membranelle, attached to inner posterior surface of the velum; second ring of cilia, found between membranelle and outer surface of the adhesive disc, are more delicate and approximately half as long as those forming the membranelle. Adhesive disc is a deep saucer-shaped organelle, ventral in position,

bordered on the dorsal side by the denticulate ring and on the posterior side by the inner row of cilia; diameter of adhesive disc ranges from 18–32  $\mu$ ; striae, present on inner and outer walls of the disc, are argento-philic. Denticulate ring non-argentophilic; diameter of the ring varies from 14–22  $\mu$ ; denticles of the ring with hooks on outer border and slender rays on inner border, joined together by triangular projections (Text-fig. 4); number of hooks varies from 21–31. Macronucleus is typically horse-shoe



Text-fig. 1. *Trichodina spheroidesi*. Side view.  $\times 950$ . Semi-diagrammatic reconstruction from hematoxylin and silver nitrate preparations. Ad. C., adoral cilia; V., vestibulum; Ma., macronucleus; C. V., contractile vacuole; Mi., micronucleus; D. R., denticulate ring; Ad. D., adhesive disc; Ve., velum; I. C., inner ring of aboral cilia; Ab. C., outer ring of aboral cilia.

shaped, with comparatively few basophilic granules; it lies in the posterior half of the cell, parallel to the dorsal plane of the adhesive disc; the open ends of the macronucleus extend to the oral side and surround the descending portion of the gullet. Contractile vacuole lies close to the descending portion of the vestibulum and during trophic life, fission and post-conjugative reorganization, it is found in the posterior half of the cell. Trophic micronucleus small, lies close to the left tip of the macronucleus; during conjugation its position is variable.

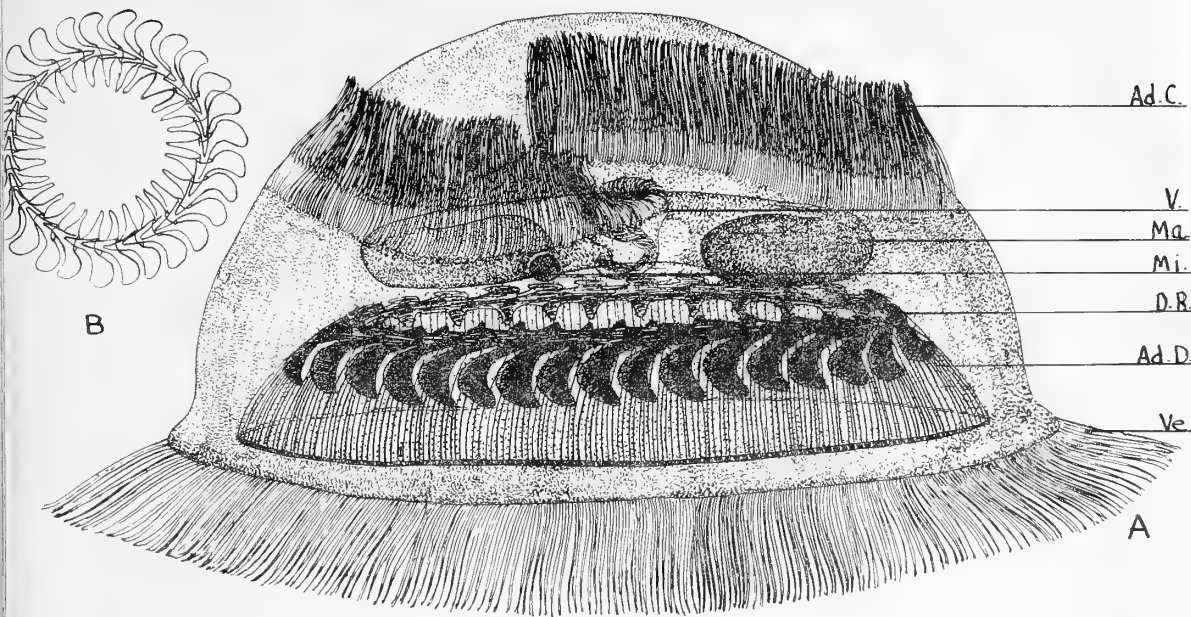
**Remarks:** Many individuals of this species were found to be infected with the suctorian parasite, *Endosphaera engelmanni*. In such cases, position of the nuclei and other cytoplasmic contents may be greatly displaced. The above description is based on several hundred normal ciliates. *Trichodina spheroidesi* is distinguished from other *Trichodina* described from marine fishes by the presence of the inner ring of aboral cilia.

#### *Trichodina halli* sp. nov.

(Text-fig. 2).

**Description:** Hemisphere or dome-shaped organisms. Diameter, taken at the base,





Text-fig. 2. A. *Trichodina halli*. Side view.  $\times 950$ . Semi-diagrammatic reconstruction from hematoxylin and silver nitrate preparations. Legend same as in Text-fig. 1. Note the absence of inner aboral ring of cilia. B. Denticulate ring.  $\times 475$ .

ranges from 45–86  $\mu$ . Adoral cilia present, similar in arrangement and extent to *T. spheroidesi*. Only one ring of aboral cilia evident; membranelle absent. Disc diameter varies from 41–81  $\mu$ ; striae present in two layers. Denticulate ring thicker than in *T. spheroidesi*; diameter ranging from 30–54  $\mu$ ; denticles fitted together by the insertion of a cone-shaped protuberance of one denticle into a corresponding depression in adjacent one (Text-fig. 2, B). Number of hooks varies from 26–34; hooks shaped and curved like a ship's propellor blade and joined to the denticles at an angle so that when observed on edge the broad area is not evident and they appear to be crescent shaped. Macronucleus as in *T. spheroidesi*, except that arms are longer and there are more basophilic granules present. Position of the macronucleus and other structures typical.

**Remarks:** *Trichodina halli* can be distinguished from *T. spheroidesi* in the following ways: (1) size of organism and organelles considerably larger, (2) ratio of disc diameter to the diameter of the organism as a whole is less, (3) denticulate ring thicker, (4) shape and arrangement of denticles and hooks entirely different, (5) longer arms of the macronucleus, and (6) lack of inner ring of aboral cilia.

The variation in size of both *T. spheroidesi* and *T. halli* suggests that other species of *Trichodina* reported in recent years may have presented a like variation in range of

measurement if sufficient numbers were studied. A review of the reported species shows that in very few instances was this range adequately determined. In the table below a comparison of measurements of various structures of *T. spheroidesi* and *T. halli* with the available data of some previously reported marine species is made. As may be seen from this table all the species, except *T. halli*, fall within the size range of *T. spheroidesi*. The distinguishing features of most of these forms consist mainly in host specificity (?) and minor variations as to shape, ciliary pattern, nature of adhesive disc and denticulate ring. Since such information is not given in sufficient detail these organisms cannot be keyed out.

TABLE I.

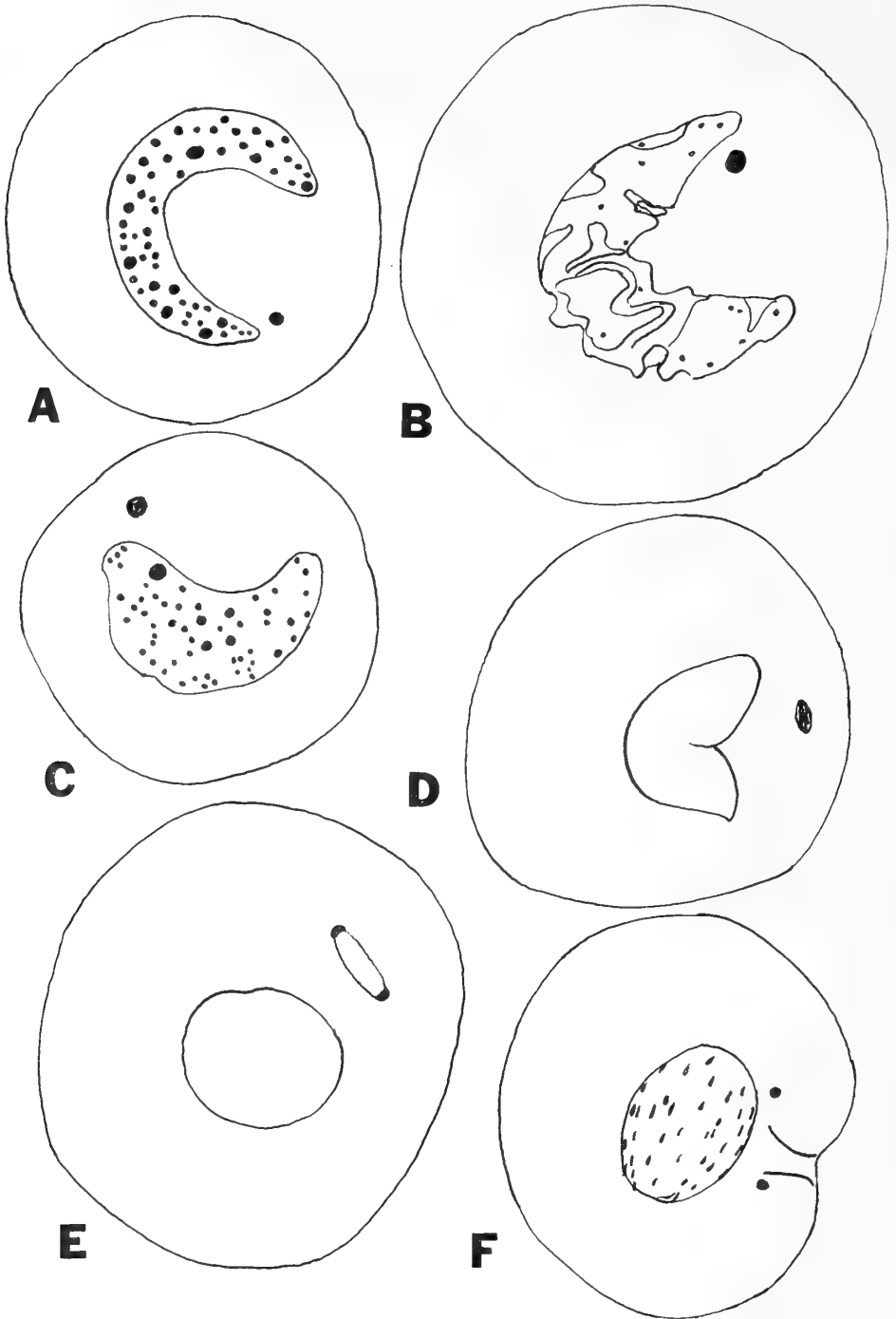
Measurements (in mm.) for *Trichodina* from Marine Fishes.

Species	Height	Width	Disc Dia.	Ring Dia.	Hook No.
<i>T. blenni</i>	20–32	40–45	24–27		24–32
<i>T. clini</i>	20	37	20		24
<i>T. cheilodichthys</i>	19–27	30–45	19–32		30
<i>T. mugilis</i>	14–20	33–44	23–28		32
<i>T. fariai</i>	32	40		20 42	24–28
<i>T. labrorum</i>	18–22	30–34			21
<i>T. spheroidesi</i>	12–42	17–54	18–32	14–22	21–31
<i>T. halli</i>		45–86	41–81	30–54	26–34

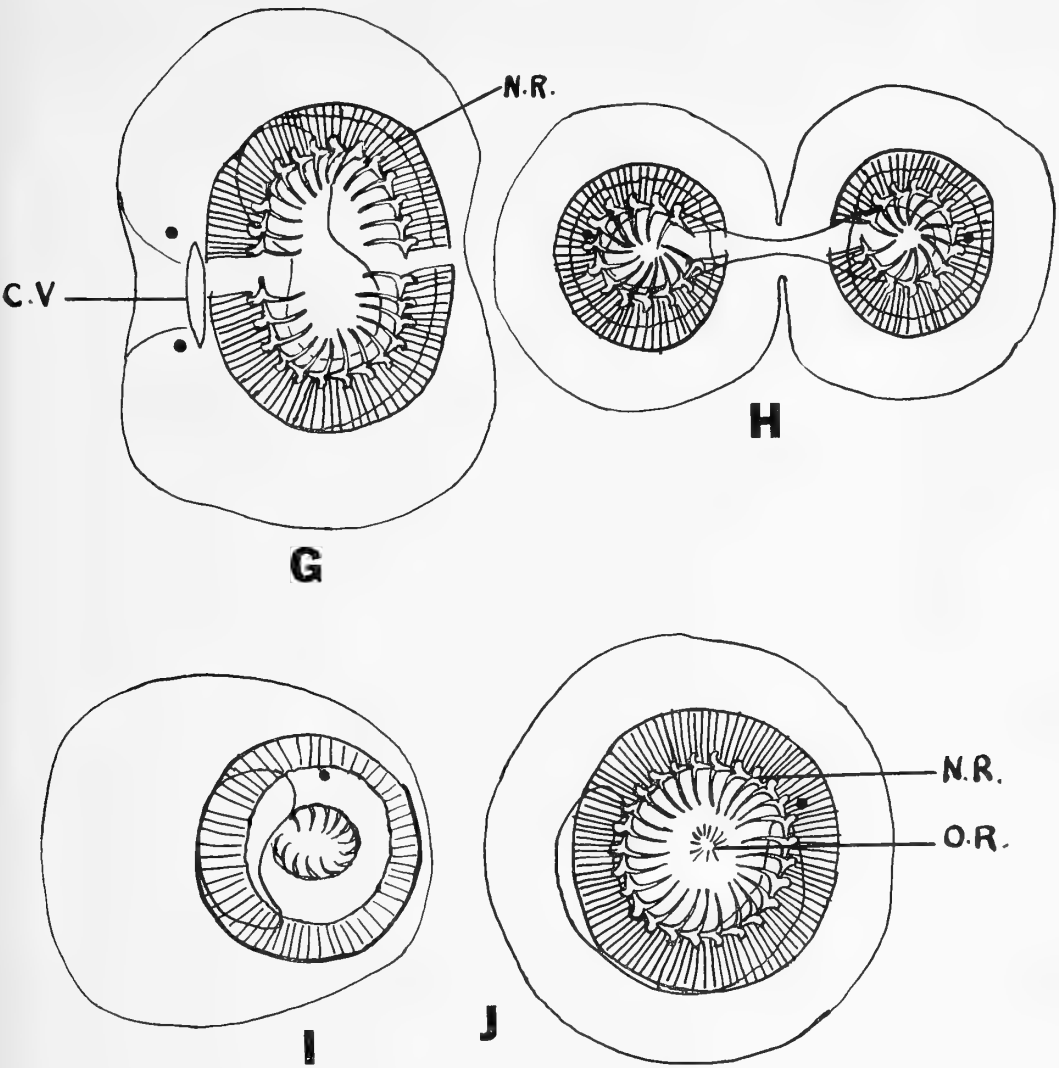
#### BINARY FISSION IN *Trichodina spheroidesi*.

(Text-figs. 3 & 4).

The stages of fission in *T. spheroidesi* correspond very closely to those described by Diller (1928) for the species of *Tricho-*



Text-fig. 3. Binary fission in *Trichodina spheroidesi*.  $\times 950$ . From iron-hematoxylin preparations. A, trophic stage; B, macronucleus in stage of contraction; C, D, and E, further contraction of the macronucleus; B and C, note swelling of micronucleus; D, micronucleus in metaphase; E, telophase; F, completed micronuclear division.



Text-fig. 4. *Trichodina spheroidesi*.  $\times 950$ . Iron-hematoxylin preparations. G, H, I, J, binary fission stages showing the final division of the macronucleus and the reorganization of the denticulate ring. C. V., contractile vacuole; N. R., new ring; O. R., old ring.

*dina* from tadpoles. The trophomacronucleus undergoes vacuolization and clefts appear in the ground substance (Text-fig. 3, B). The macronucleus begins to condense while the chromatin granules, large in the trophic stage, become smaller in size and randomly distributed in the matrix. As the macronucleus contracts further, the micronucleus swells, eventually becoming spheroidal, then divides mitotically (Text-fig. 3, C, D, E). A metaphase stage of a dividing micronucleus is shown in Text-fig. 3 D. The mitotic division continues as the macronucleus pulls apart, and two daughter micronuclei are formed before the macronucleus is com-

pletely divided (Text-fig. 3, F; Text-fig. 4, G). Plasmotomy takes place about the time of the late telophase. A stricture appears in the ventral portion of the organism, and the adhesive disc and denticulate ring separate into approximately equal halves (Text-fig. 4, G, H). Final cleavage of the macronucleus takes place and two daughter cells are formed (Text-fig. 4, H). Peshkowsky (1923) reported that during division of *Trichodina steinii* and *T. mitra* the adoral cilia, gullet and contractile vacuole are absorbed. Careful study of the silver impregnated material, however, leads the

writers to believe that the adoral and the aboral zones of cilia, in *T. spheroidesi* at least, are retained throughout division. The fate of the vestibulum and the vestibular cilia could not be traced. In specimens stained with hematoxylin, it was observed that the contractile vacuole is retained also during cell division. It appears to cleave concomitantly with the cleavage of the macronucleus (Text-fig. 4, G).

The anlage of the new denticulate ring (corona) is laid down as a delicate ring close to the posterior border of the adhesive disc before the onset of cell division (Text-fig. 4, G). This confirms the observations of Diller (1928). After the formation of the daughter cells the new corona gradually develops its denticles and hooks and takes up a more dorsal position on the adhesive disc. The rays are the last structure to be formed in the ring. Half of the old ring, carried over after cell division by each daughter cell, is pushed into the ventral plug of the cytoplasm between the aperture of the adhesive disc. Here it is slowly resorbed (Text-fig. 4, I, J).

#### CONJUGATION IN *Trichodina spheroidesi*.

(Pl. I-III).

Conjugation in *T. spheroidesi* is anisogamous and the process is very similar to that reported by Maupas (1888) for *Vorticella nebulifera* (see also Doflein, 1927). The aboral surface of the microconjugant is fitted over the adoral surface of the macroconjugant (Pls. I, II). They may or may not be oriented in the same direction. After the conjugants have assumed their respective positions, the micronucleus of each begins to swell, eventually becomes vesicular and passes from the original posterior position to a more central location in the cell (Pl. I, Figs. 1-3). The macronucleus begins to show signs of vacuolization (Pl. I, Fig. 2).

At the time of spindle formation, the macronucleus twists and pulls apart into large coarse fragments (Pl. I, Fig. 3). These pieces continue to break up into smaller and smaller parts until minute spherical bodies with deeply staining granules are formed (Pl. I, Figs. 4, 5, 6, 7, 8; Pl. II, Fig. 9).

Micronuclear activity immediately preceding the metaphase period is not clearly defined (Pl. I, Fig. 4). It is possible that the micronuclei have a decreased affinity for iron-hematoxylin stain during these stages. The metaphase spindle, however, is clear and granular chromosomes can be identified about the center (Pl. I, Fig. 5). During the final fragmentation of the macronucleus, two micronuclear divisions take place in each conjugant (Pl. II, Fig. 10).

It is of interest to point out here that conjugation in *T. spheroidesi* differs from

conjugation in *Vorticella nebulifera* in that there are only two micronuclear divisions in each conjugant instead of three.

Protoplasmic continuity is established between the conjugating individuals (Pl. II, Fig. 11), and the contents from the smaller individual pass into the larger one (Pl. II, Fig. 12). It is assumed that the gametic nuclei (Pl. II, Fig. 10) then combine to form the synkaryon, and the remaining nuclei are resorbed. The remains of the microconjugant collapse and the ensuing processes of conjugation are confined to the single large exconjugant (Pl. II, Fig. 13).

At the onset of its first division, the zygotic nucleus develops a larger spindle than any of the dividing nuclei in the early stages of conjugation. It is assumed that three mitotic divisions subsequently occur, resulting in eight micronuclei. Seven of these become the macronuclear anlage and one the functional micronucleus (Pl. II, Figs. 14, 15). The functional micronucleus divides (Pl. II, Fig. 15) and in the cell division which takes place, the macronuclear anlage are distributed between the daughter individuals (Pl. III). The most frequent distribution is three and four (Pl. III, Figs. 16, 17). However, the distribution may sometimes be two and five (Pl. III, Figs. 18, 19) or one and six. Cell division continues until each of the daughter cells formed contain one macronuclear anlage (Pl. III, Fig. 20). The macronucleus then increases in size and develops its characteristic horse-shoe shape.

Reorganization of the denticulate ring occurs in the macroconjugant shortly after the fusion of the protoplasmic contents of the conjugants has occurred. Figures 12 and 13 of Plate II show the newly formed ring together with the remains of the old denticulate ring. It should be pointed out that the original ring is present in preceding stages but is not shown in the figures for sake of clarity. It is of interest to note that the number of denticles in the new ring is invariably the same as the number present in the old ring. Such structures as the gullet, vacuole and cilia are present throughout conjugation.

#### DISCUSSION.

*Trichodina spheroidesi* is distinguished from other *Trichodina* of marine fishes by the presence of the inner ring of aboral cilia. Wetzel (1927) and Precht (1935) reported a similar observation for *T. pediculus* and *T. scoploplontis*, respectively.

The double layer of striae in the adhesive disc observed by the writers in the two forms from the puffers have been previously reported by Mueller (1932, 1938) for *Trichodina renicola* and *Vauchomia nephritica*. Mueller (1938) refers to the inner group of striae as the posterior hard rays and the outer group as the anterior soft

rays. He further commented that the soft rays comprise a system of myonemes which connect with the posterior girdle of cilia. This duplex nature of the striae Mueller featured to distinguish members of the Trichodinidae found in the urinary tract of fishes (e.g., *T. renicola* and *V. nephritica* from *Esox niger* and *Esox masquinongy*, respectively) from those found on the gills of certain fresh-water fishes reported by him in 1937. In the ciliates from the gills only the hard rays were present in the striated ring. However, the occurrence of double striations in the forms described by the writers suggests that this feature may be more widespread than heretofore has been observed.

The similarity of conjugation in *Trichodina pediculus* to that of certain members of the Vorticellidae was first pointed out by Busch (1855). Stages in conjugation among certain of the Urceolariidae have since been recorded and the same comparison made. Caullery & Mesnil (1915) reported stages in conjugation in *Trichodina patellae* (Cuenot) from a species of fresh-water mollusc. Peshkowsky (1923) described conjugation in *T. steinii* and commented that this process was similar in all essential features to that observed in the Vorticellidae. Anisogamous conjugation was described by Zich (1928) for *Urceolaria korschelti*, and by Hunter (1936) for two types of *Trichodina* found in the intestine of sea-cucumbers. Diller (1928) described in detail endomixis in *Trichodina* from tadpoles. He suggested that some of the evidence of conjugation presented by Caullery & Mesnil, Peshkowsky and others were most likely stages in endomixis. The endomictic stages described by Diller, however, conform closely to the nuclear reorganization in the post-conjugative stages described for *Trichodina spheroidesi*. Diller makes a distinction between endomictic individuals and conjugating forms on the basis of differences in shape of macronuclear fragments. Since the fragments in Diller's material are not unlike those observed in some of the stages in conjugation in *T. spheroidesi* this distinction cannot be supported. Any other differences that Diller may have noted are, in all probability, the result of examining too few samples of conjugation which he stated was present in his material. That he may have misinterpreted post-conjugation for endomixis is supported further by the similarity of his figure (Pl. II, Fig. 14) of the first micronuclear division to the figure of the zygote nucleus in *Vorticella nebulifera* shown by Maupas (1888) (see Doflein, Fig. 310) and in *Trichodina spheroidesi* (Pl. II, Fig. 13).

## SUMMARY.

1. *Trichodina spheroidesi* and *T. halli* spp. nov. from the gills and skin of puffers (*Spheroides maculatus*) and other marine fishes from the New Jersey and the New York coast are described.
2. The processes of fission and conjugation are described for *T. spheroidesi*.

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## EXPLANATION OF THE PLATES.

Anisogamous conjugation in *Trichodina spheroidesi*. All figures drawn from material stained with iron-hematoxylin.  $\times 950$ .

### PLATE I.

- Fig. 1. Start of conjugation.  
 Fig. 2. Macronucleus in the process of fragmentation. Note lumping of nuclear material. Micronucleus in pre-metaphase stages of meiosis.  
 Fig. 3. First macronuclear fragmentation. Micronucleus still in pre-metaphase stage.  
 Fig. 4. Further macronuclear fragmentation.  
 Fig. 5. Metaphase of meiotic nucleus clearly evident. Fragmentation of the macronucleus continues.  
 Figs. 6, 7, 8. Continued meiotic division and completion of fragmentation of the macronucleus into many spherical and oval shaped bodies of various size.

### PLATE II.

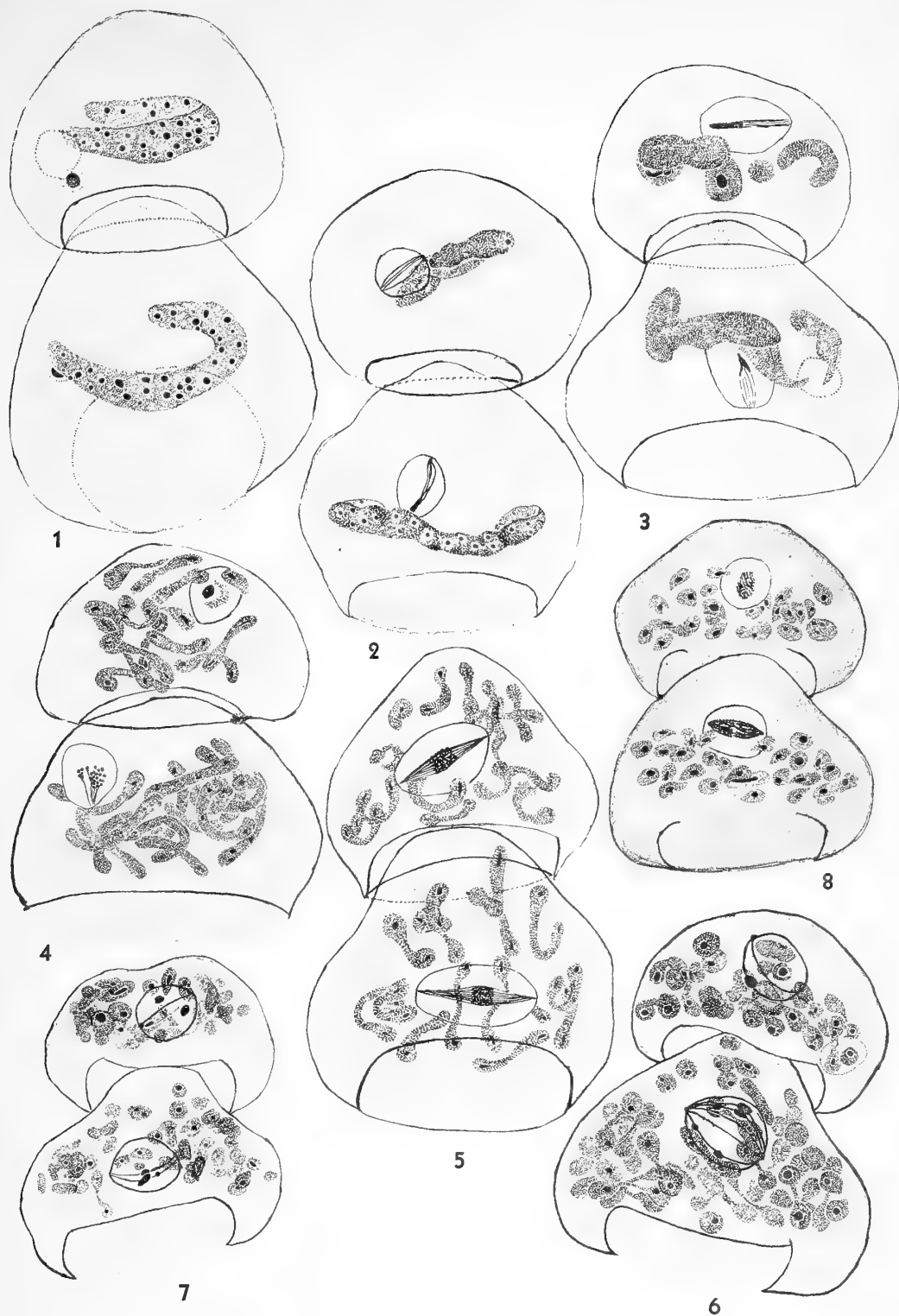
- Fig. 9. Continuance of the meiotic process seen in Fig. 8.  
 Fig. 10. Second micronuclear division. Note persistent gametic micronucleus and the degeneration of other three micronuclei in each conjugant.  
 Fig. 11. Gametic nuclei in an early stage of fusion to give rise to the synkaryon. The other micronuclei completely disappeared. Note the completion of cyto-

plasmic continuity between the conjugants.

- Fig. 12. The cytoplasmic contents of the microconjugant pass into the macroconjugant. The new denticulate ring develops while the old ring is resorbed. In this individual the macronuclear fragments are coarser than in the preceding stage.  
 Fig. 13. Post-conjugant stage. Macroconjugant with large zygotic nucleus in metaphase stage. New denticulate ring and remnant of the old ring still present.  
 Fig. 14. Initial stage in development of the macronuclear anlage. There are seven of these larger bodies present, indicating that three divisions of the zygotic nucleus had taken place.  
 Fig. 15. Further development of the macronuclear anlage. The start of the first binary fission. Micronucleus in metaphase.

### PLATE III.

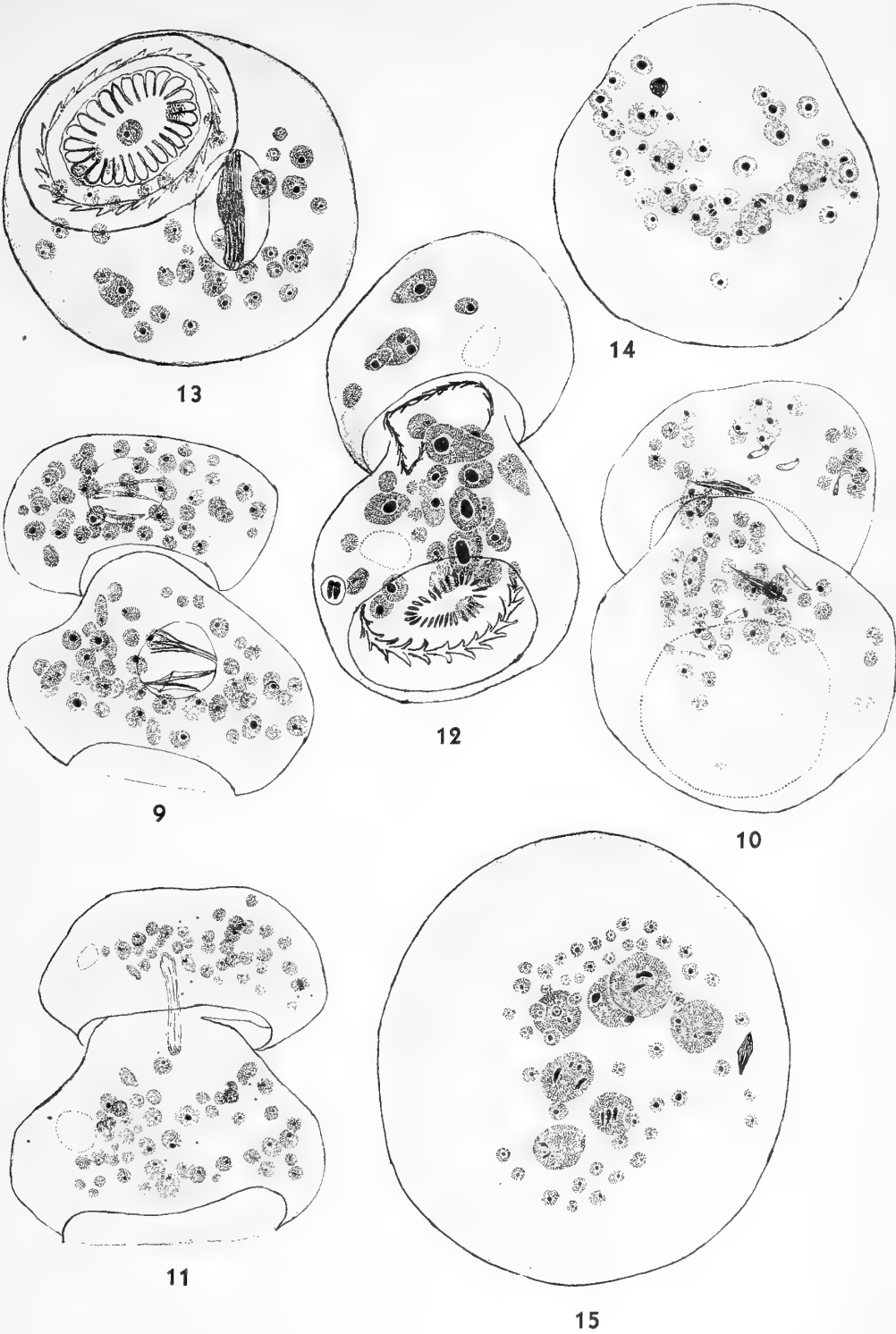
- Figs. 16, 17. Daughter cells showing the three and four macronuclear anlage distribution.  
 Figs. 18, 19. A two and five distribution of macronuclear material.  
 Fig. 20. Each cell will continue to divide until only a single macronuclear anlage is present in each individual. The last step in this process is shown in this figure.



TRICHODINA SPHEROIDESEI AND TRICHODINA HALLI SPP. NOV. PARASITIC ON THE GILLS AND SKIN OF MARINE FISHES, WITH SPECIAL REFERENCE TO THE LIFE-HISTORY OF *T. SPHEROIDESEI*.





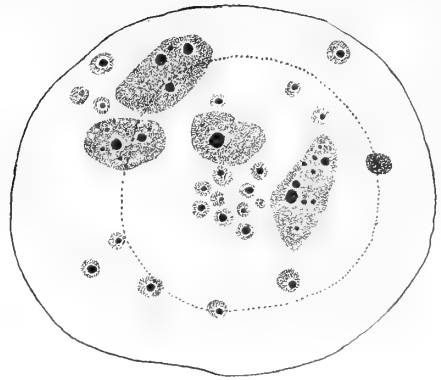


TRICHODINA SPHEROIDESI AND TRICHODINA HALLI SPP. NOV. PARASITIC ON THE GILLS AND SKIN OF MARINE FISHES, WITH SPECIAL REFERENCE TO THE LIFE-HISTORY OF T. SPHEROIDESI.

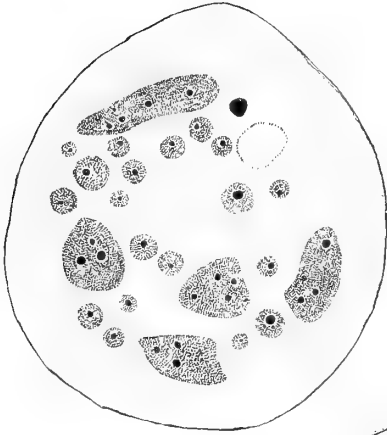




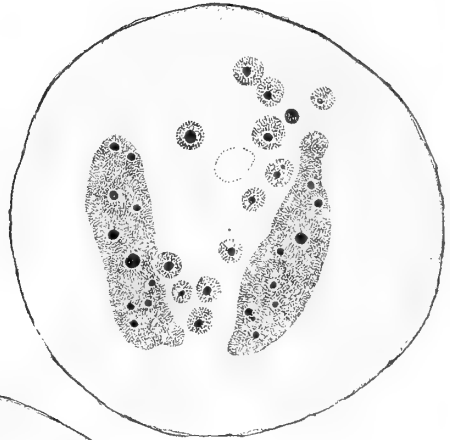
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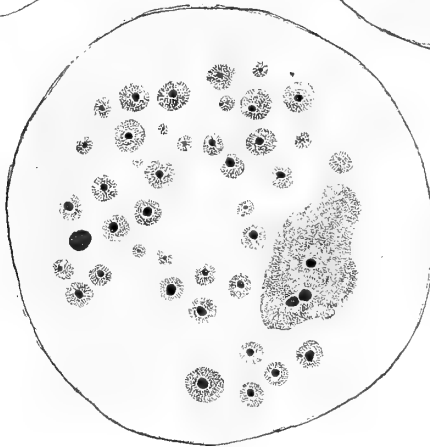
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TRICHODINA SPHEROIDESI AND TRICHODINA HALLI SPP. NOV. PARASITIC ON THE GILLS AND SKIN  
OF MARINE FISHES, WITH SPECIAL REFERENCE TO THE LIFE-HISTORY OF T. SPHEROIDESI.



13.

Mortality of Albino Embryos and Aberrant Mendelian Ratios in Certain Broods of *Xiphophorus hellerii*.<sup>1</sup>

MYRON GORDON

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(Text-figure 1).

In a previous publication,<sup>2</sup> the author has shown that when the albino swordtail is mated with the golden variety, their offspring resemble neither parent but revert to the ancestral gray coloration of the wild species.

The author showed further that when the gray offspring of the above mating reached maturity and were mated together, brother to sister, the second generation population consisted of three color classes: 202 were "wild" gray, 65 were golden and 67 were albino. These frequencies approached the theoretical 9:3:4 ratio and were interpreted on the basis of the recombination of two independent autosomal factors: *St I* for "wild" gray, *st I* for golden and *St i* and *st i* for albino.

To get the above data the results of four matings were pooled, as Table I will show.

TABLE I.  
Second Generation Offspring of Gray (*Stst Ii*) Swordtails.

Female No.	Gray	Golden	Albino
70-4	37	12	8
70-5	38	13	6
70-6	50	15	20
70-7	77	25	33
Totals observed	202	65	67
expected	188	63	83

It was noted that there was a deficiency of albinos in the above totals, particularly in broods from females 70-4 and 70-5, yet the two independent factor hypothesis seemed most appropriate in explaining the results. This was confirmed when the Chi-Square test for significance was applied to the pooled data; the value of Chi-Square was

found to be 4.18. However the value of Chi-Square for the first two broods alone was 9.84 and indicates the deviations found here cannot be attributed to chance.

Broods were obtained from three additional females after mating with their gray brothers. The three females, 70-8, 70-9 and 70-10, yielded ratios so obviously aberrant that counts of their young were not included in the original presentation because it was thought, at the time, that a contaminating factor was involved in this portion of the experiment. Further study was undertaken to account for these unusual results.

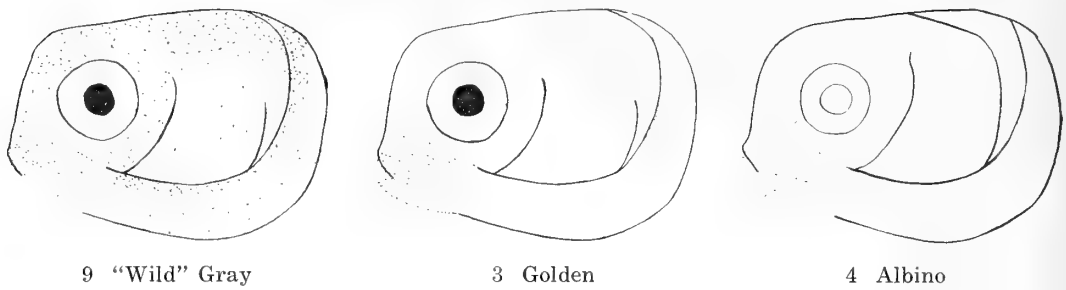
Reports from the laboratories of other workers and from our results as indicated in Table I pointed to a deficiency of albinos in genetic tests. This was attributed to the constitutional weakness of the albino individuals. It was noted, for instance, that if the fishes of a brood are counted soon after birth and again after two months, the death rate of albinos is greater than that of the other color varieties.

From this evidence it was suspected that the weakness of the albinos may be manifest early, perhaps in their embryonic stages of development. The three additional females, 70-8, 70-9 and 70-10, that produced hardly any albinos in their first broods (see Table II), were killed three weeks after giving birth to their last brood. The females were dissected, their embryos were removed and counts were made of them. In each case an appropriate proportion of albinos was found among the gray and golden embryos. This may be seen in Table II.

DISCUSSION AND CONCLUSIONS.

It is obvious that the numbers of albinos are decidedly deficient among the young fishes from females 70-8, 70-9 and 70-10; the extremely high value of Chi-Square, 42.46, indicates that the results obtained are not due to chance variation alone. On the other hand, the numbers of albinos

<sup>1</sup> I wish to express my thanks to the Department of Birds of the American Museum of Natural History for the use of their laboratory in the Whitney Wing of the Museum.  
<sup>2</sup> Back to their Ancestors, *Journal of Heredity*, 32: 385-390, 1941.



Text-fig. 1. Embryos from gray females mated to gray males.

TABLE II.  
Offspring of Gray (*Stst li*) Swordtails.

Female No.	Gray	Golden	Albino	
70-8	38	11	2	Young
	35	10	13	Embryos
70-9	45	10	1	Young
	40	9	12	Embryos
70-10	58	18	1	Young
	40	12	17	Embryos
Totals:				
Observed	141	39	4	Young
Expected	103.5	34.5	46	
Observed	115	31	42	Embryos
Expected	106	35	47	

found among the embryos of the same females are in close harmony with expectancy. The slight deviations found may be at-

tributed to chance, for the Chi-Square value is low, 1.75.

In light of all the data, the gray females tested may be divided into three groups according to their ability to produce viable albino swordtails. Females 70-8, 70-9 and 70-10 fail in this respect almost completely; females 70-4 and 70-5 fail to produce an adequate number according to expectancy; females 70-6 and 70-7 have the ability to produce viable albino young in normal numbers.

Thus the deficiency of albinos in certain broods must be attributed not only to the low viability of the albinos themselves but also to some failure in the ability of the albinos' mothers to carry their complete broods through to birth.

## 14.

## The Schooling Behavior of Mackerel: A Preliminary Experimental Analysis.

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(Plate I).

### INTRODUCTION.

As indicated in the comprehensive review of the field by Allee (1931), animal aggregations and their significance have attracted increasing critical analysis in recent years. Curiously, the fish school—one of the most striking examples of well-integrated animal aggregations—has received remarkably meager critical attention. Spooner (1931) and Breder & Nigrelli (1935), considering various aspects of schooling in fishes, have noted this unfortunate lack of literature. Some notes on the schooling behavior of the herring, *Clupea harengus* L., by Newman (1876), constitute one of the earliest publications in this field. Nevertheless, Parr (1927) after a fifty year interval had a virtually clear field for his theoretical analysis of the schooling behavior of mackerel.

Fishes which do not school and have no visible aggregating tendency have been considered "non-social" forms. However, it is unwise to so classify a form which manifests no obvious social tendencies. Statistical evidence has demonstrated that the goldfish, which had been summarily thus dismissed, manifested a definite group effect; isolated individuals were found to have a higher rate of locomotor activity and oxygen consumption than did grouped goldfishes (Schuett, 1934; Escobar, Minahan & Shaw, 1936; Breder & Nigrelli, 1938; Shlaifer, 1938). Hence, social tendencies may be relatively obscure and not readily determined by casual observation.

At the extremes, it is a relatively simple matter to differentiate between a loosely aggregating fish and a closely schooling one. However, in many cases it is exceedingly difficult to determine whether a fish should be considered a closely aggregating form or a loosely schooling one. The mackerel imposes no such difficulties. It remains in dense schools throughout life, except for possible dispersal at night. It is difficult to

think of an instance, at least among vertebrates, in which individuality is as completely lost as it is in a mackerel or herring school.

Parr (1927) subjected the mackerel school to critical theoretical analysis. Several interesting conclusions were reached which will be considered later. His report, however, contains relatively little experimental data. It is the purpose of this report to treat the phenomenon experimentally and, wherever possible, to attempt correlation with Parr's theoretical conclusions.

The writer wishes to express his deep appreciation to the U. S. Fish and Wildlife Service at whose Woods Hole station the experiments were performed; also to Dr. R. Buchsbaum whose photographic skill is responsible for the figures in the plate.

### EXPERIMENTAL STUDY.

*Number of Individuals Needed to Form a School:* The experimental animals used in these and subsequent tests were 8-inch specimens of the chub mackerel, *Pneumatophorus grex* (Mitchill). Originally caught in the waters off Woods Hole, they were subsequently kept in appropriately large tanks in the laboratory. Several days were allowed for acclimatization before the animals were used. Two tanks were employed for experimental purposes. One was a rectangular assembled aquarium with transparent glass sides whose dimensions were 36" by 15" and 17" deep. The other was a rectangular wooden tank 44" by 23" and 9.5" deep. Sea water was kept running through these tanks at all times at a fairly rapid rate. The average oxygen content was 5.60 cc. per liter and the temperature range was 18–20 degrees C. In general, the mackerel survived well. Of those that died, many expired during the course of acclimatization in the laboratory. Most of those which survived this period lived for several weeks in no apparent distress.

Repeated experiments demonstrate that

two individuals suffice to form a mackerel school. If two fishes are removed from a group and placed in the wooden tank they immediately school, i.e., swim about the tank nearly always in line with each other. If one mackerel is kept isolated in a tank and another is grouped with it, they immediately school. Apparently, the fish that first becomes aware of the presence of the other initiates the schooling reaction. Whether this will be the original fish or the introduced one is purely a matter of chance for it will be one or the other 50% of the time. Other fishes added to this group of two immediately join the school.

Thus, only two individuals are required to begin the formation of a mackerel school which is, however, better integrated if composed of many individuals.

Breder & Nigrelli (1935) found that two sunfishes, *Lepomis auritus*, grouped together in a tank "aggregate" with each other after two days. Shlaifer (1938) demonstrated that the oxygen consumption and locomotor activity of an isolated goldfish is significantly higher than is that of an individual in a group of two.

It would seem, at least in the cases listed above, that there is a much greater psychic difference between an isolated fish and one in a group of two than between the latter and an individual in a much larger group.

*Effect of Various Types of Blinding:* Parr (1927) found that when chub mackerel were blinded by the application of vaseline and lampblack to the eye, they did not school or mill. Blinded catfishes do not aggregate (Bowen, 1931) nor do blinded sunfishes (Breder & Nigrelli, 1935). Grouped goldfishes which are normally less active than isolated individuals lose this group effect when they are blinded (Shlaifer, 1939). These results as well as other lines of evidence indicate the importance of vision in integrating social behavior in fishes.

The experiments described below were designed to repeat and to extend the original work of Parr (1927) on this species. Mackerel were blinded by piercing the cornea and were kept in the wooden tank described above. One day was allowed for recovery from operative shock. Blindness was ascertained by appropriate tests, e.g., failure to avoid a net, etc. All results noted for the various blinding experiments were confirmed by repeated tests. As controls, the area in the vicinity of the eye of non-blinded mackerel was pierced by the same instrument used for blinding, thus approximating similar conditions of shock. In no case did control individuals fail to school when grouped.

If an individual is blinded on one eye and subsequently grouped with six schooling mackerel, it immediately joins the school.

In fact, if only three minutes are allowed for recovery from the shock of the operation instead of the customary day, it also rejoins the school immediately. This half-blinded fish succeeds in maintaining its orientation with respect to the rest of the school fairly well. Sudden turns by the normal animals to the blinded side of the experimental fish may result in temporary loss of integration of that animal with the school; however, it is quickly recovered.

If a mackerel is subjected to bilateral blinding, it makes no attempt to join the school. Occasionally its random movements about the tank may disrupt the smooth integration of the normal school but only for a moment.

The grouping of a normal fish with a half-blinded one results in a schooling reaction. In general, the unilaterally blinded animal will orient itself so that the intact eye side is the one nearest the normal fish. Sudden turns by either animal will initiate a turn in the other, thus maintaining the school. If the half-blinded fish is then blinded on the other eye, the school disintegrates. There is, of course, no reaction by the sightless form to the normal one. However, it might be expected, inasmuch as there is no other mackerel in the tank but the blinded individual, that the normal fish would attempt to school with it. This is not the case.

Sightless mackerel do not swim in a typically normal manner; movement is slower and less uniform. Apparently, normal swimming movement is of great importance in the schooling reaction of mackerel.

If two mackerel are blinded on the same eye, a school obtains though it is not as well integrated as is a school of two normal individuals or one normal and one half-blinded form. In this case the maintenance of the school is dependent upon the behavior of the fish whose intact eye side is nearest the other animal whose swimming movement is apparently sufficiently normal to evoke a schooling reaction by the mackerel which is in visual contact with it. We are presented with the unusual case of a school of two fishes, one of which plays a passive role. Sudden turns and changes in direction may reverse the role of either fish. The mackerel which sees the other member of the group of two usually follows the turns of the passive partner. On occasion, however, it may initiate a turn, in which case the school is broken for a second or so until one individual finds the other.

If, in a group of two, one mackerel is blinded on its left eye and the other on its right one, schooling behavior is very erratic. If their blinded sides face each other no reaction obtains; if not, they school, though the school is likely to be broken by a sudden sharp turn by one animal which results in



their blinded sides facing each other again.

A totally blinded fish grouped with a half-blinded one evokes no good schooling reaction by virtue of the abnormal movement of the former. Two totally blinded individuals grouped together will swim at random and may collide.

Confirming Parr's data (1927), three mackerel blinded in both eyes and placed in an exhibition tank containing a large school of mackerel swim aimlessly and make no attempt to join the group.

The results obtained demonstrate the role of vision. Also indicated is the importance of normal swimming movement.

Any experiment in which visual response is eliminated through blinding suffers from the criticism that the normal physiological state of the animal may be disturbed. This may be true even when a period deemed to be sufficient for recovery from shock obtains. A more natural condition is darkness and a description of the behavior of mackerel in this state follows.

*The Effect of Darkness on Schooling:* Newman (1876) finds that the closely schooling herring, *Clupea harengus*, break up completely at night in a tank in captivity, each fish taking an independent path. The school reforms in the presence of sufficient light. Breder (1929) reports that compact schools of *Jenkinsia*, also a member of the family Clupeidae, are dispersed at night. Bowen (1931) finds that aggregations of catfishes are dispersed in darkness. Breder & Nigrelli (1935) report that aggregations of the sunfish, *Lepomis auritus*, break up with the coming of night. Shlaifer (1939) finds that the effect of grouping (decreased oxygen consumption) on goldfishes disappears in total darkness.

The behavior of mackerel in darkness was investigated by two procedures, one observational, the other photographic. One of the exhibition tanks of the Aquarium at the Woods Hole station of the U. S. Fish and Wildlife Service contains a school of forty to fifty 8-inch chub mackerel, as well as a turtle, flounder, blackfish, and skate. The tank, rectangular in shape, is 6.5 feet by 4 feet and 3 feet deep. Three of the vertical sides are composed of stone and cement and the fourth of transparent glass.

The lights in the Aquarium were always off at night and after 9 p.m. the room was quite dark. The observer, looking at the tank from above or standing next to the transparent glass side, could see nothing in the tank; in fact, one's hand held two inches from the eye was quite invisible. For several hours at night during several consecutive evenings observations were made on the schooling behavior of the mackerel in this state of darkness. At half-hour intervals a flashlight beam was directed at the bottom of the exhibition tank for only one or two

seconds. If maintained longer, the fishes would react to the light, weak though it was, by forming a dense school. Hence, it was necessary to form an impression of the aggregating condition of the group in this very short time. The general impression gathered by these observations was that the school was fairly well dispersed. The fishes were never found to be closely schooling or milling but neither were they swimming about the tank at random as Newman (1876) reported for the herring in darkness. The mackerel swam in an elliptical orbit more or less in the same direction but with considerably greater distances between individuals than is found in a normal school in the light. Considering the number of individuals, the size of the tank, and the tendency of mackerel to swim in a uniform way for hours unless disturbed, the observed state of the school is probably what is to be expected in the absence of visual integration. Further experiments are planned along these lines.

The mackerel eye is apparently capable of detecting similarly moving forms at very low light intensities for when they could just barely be seen they were in fairly compact schools. This is in contrast to the findings of Breder & Nigrelli (1935) for sunfish aggregations which break up when they can still be seen distinctly. Another interesting fact is that the mackerel also is capable, apparently, of seeing in light at the deep red end of the spectrum. When a Wratten Series II Safelight, which transmits light in the deep red from about 650 $\mu$ . to 700 $\mu$ ., was suspended at night over the tank several inches from the water surface in otherwise total darkness, the mackerel formed fairly compact schools and mills. (See Plate I, Fig. 3.)

The observational method described above is open to the criticism that the observer's reaction must be instantaneous and is subjective. Accordingly, a series of flash-bulb photographs was made of the mackerel group in artificial light and in total darkness. These flash-bulb photographs are taken in a fraction of a second, much too fast for any disturbance caused by the blinding flash of light to be recorded in the photograph. The school was photographed from the side through the transparent glass. Darkness shots were taken only after a period of at least 15 consecutive minutes of darkness following the small amount of illumination from a flashlight incident to setting up the equipment. Darkness set in at about 9 p.m. and the first photograph was usually taken at about 10 p.m. Plate I contains two photographs which represent typical results. Fig. 1 is a compact mackerel school under fairly strong artificial light. Fig. 2 was taken in total darkness at about 10:30 p.m. The contrast in the denseness of the aggregations

is obvious and portrays the results obtained by observation.

The observational and photographic evidence reveals that mackerel schools apparently are dispersed in total darkness. However, the ability of mackerel in aquarium tanks to school at very low light intensities leaves unsolved the condition of mackerel schools in nature where dim light may obtain at night. It is the intention of the writer to pursue this matter more exhaustively in future work.

*Visual Contact:* Schlaifer (1939, 1940) found that the oxygen consumption and locomotor activity of isolated goldfishes in visual contact with others of the same species and variety was of the same order of magnitude as that of these individuals when actually members of a group. This confirmed previous results which demonstrated the visual integration of the group effect. Although darkness and blindness tests have indicated the importance of vision in the schooling behavior of mackerel, the following experiment was performed as a bit of additional evidence.

The glass tank whose dimensions have been listed above was divided in half along its length by a plate of transparent glass. One mackerel was placed on each side. After a short period of acclimatization, the two fishes tended to swim close to the dividing glass plate in line with each other. In general, the animals would turn only when they reached one end of the tank and would then swim back to the other end. If, however, one mackerel turned in the center of the tank, the fish on the other side of the glass in visual contact with it would usually also turn before reaching the end of the tank. This behavior was not invariable but occurred with sufficient frequency to be considered significant.

Thus, from three lines of evidence—blinding, darkness, and visual contact experiments—the important role of sight is demonstrated.

*Response to Form and Movement:* Spooner (1931), working with the bass, *Morone labrax*, which is a schooling form, found that individuals would be attracted to dead, mounted, specimens of the species but not to rough models. Similar results were obtained for the goldfish (Schlaifer, 1939, 1940). Thus, there is indicated that there may be a visual response to objects of the proper form though they are devoid of movement. Response to form is also reported by Breder (1929) for the schooling herring, *Jenkinsia*, and by Breder & Nigrelli (1935) for the aggregating sunfish, *Lepomis auritus*. On the other hand, many sexual behavior studies emphasize the importance of movement (Noble, 1934; Breder, 1936).

Experiments demonstrate that a mackerel isolated in a tank with freshly killed and mounted specimens placed in the normal swimming position, does not react to them. On the other hand, if another normal mackerel is introduced into the tank, the schooling reaction is immediately evoked.

Repeated experiments were performed with freshly killed mackerel which were manipulated by means of a long rod, the hooked end of which was inserted in the back of the fish. A normal mackerel was grouped with a mounted fish which was then manipulated so as to simulate a normal swimming animal. In only one case in 70 trials was there any response given to the dead specimen. Again, normal mackerel introduced into the experimental tank elicited immediate schooling. An olfactory basis for the lack of response to a dead, manipulated individual is not probable by virtue of the fact that the animals were freshly killed and were in fairly rapidly flowing water.

It may be concluded that normal swimming movement is an important factor in the schooling reaction. True, with normal movement a mackerel may be attracted by the body form of its neighbor but, in the absence of normal movement, form alone will not suffice. The importance of normal movement is further emphasized by the failure of a mackerel to school with a blinded individual which does not swim in the usual manner. Evidently, mackerel are sensitive to differences in motion which we can also detect and quite possibly to minor differences which we cannot observe. Nevertheless, further experimentation along these lines is in order. If simulation of swimming motion in a killed mackerel can be skillful enough to evoke a schooling reaction, neat checks might be obtained on response to form by altering in many ways the shape of the dead specimen.

*Response to Color:* The reaction of fishes to colors is still the subject of considerable debate. Warner (1931) criticized the lack of control of the intensity factor and deemed most of the experimental work worthy of repetition. White (1919, 1927) demonstrated that mudminnows and sticklebacks can discriminate between wave lengths and not merely intensities of light. Brown (1937) found that the large-mouthed black bass, *Huro salmoides*, responds to differences in wave lengths. Noble & Curtis (1939) demonstrated that young cichlids may be born with a greater interest in moving red discs than in moving black, blue, green or yellow ones.

Schlaifer (1939), though not differentiating between wave length and intensity, found that the group reaction in the goldfish was not in any way based on color differences or similarities. Accordingly, ex-

periments were performed with mackerel to determine whether response to color was in any way involved in the schooling behavior. Mackerel were removed from the tank and painted of various colors were applied over all of the body but the eye. They were then allowed a period of recovery from shock and were grouped in various combinations. Specimens painted blue were grouped with ones painted white, black, etc. In all cases, schooling occurred immediately with no indication whatsoever of differential response to color.

*Effect of Isolation:* Bowen (1932) found that the sight response of normal aggregating catfishes to one another was not completely eliminated in all individuals by 161 days of isolation. It was much less marked but was re-established in the course of a few minutes, usually after contact occurred. Catfishes isolated for only 52 days when grouped together showed no difference in behavior from those animals kept in a group.

Five mackerel were isolated for 20 days, the maximum time available before the laboratory closed. At the end of this period, two of the five were grouped together as were the remaining three. Schooling occurred immediately. If mature mackerel could be kept in isolation for much longer periods, it would be interesting to observe subsequent schooling behavior. Even more interesting would be the subsequent schooling reaction of mackerel reared in isolation from various early stages.

#### DISCUSSION.

The experimental results reported above confirm the data of Parr (1927) on the visual integration of the mackerel school. Further, it is seen that only two normal individuals are necessary to begin a school. The visual response is apparently not correlated with color but is with normal swimming activity. Finally, several weeks of isolation do not induce any weakening of the schooling reaction.

The fact that two individuals suffice to begin a school, at least under laboratory conditions, may have implications for larger aggregations in nature. If schools are completely dispersed at night, their reformation in daylight would be definitely facilitated by the mutual attraction of only two fishes. In fact, again granting the break up of the school at night, without a schooling response by one solitary fish to another one, it is difficult to see how schools could reform.

In reference to the apparent visual integration of fish schools, Parr (1927) indicates that schooling pelagic fishes have eyes of large size and rather scantily equipped lateral line systems. He concedes that lateral line stimuli might come into play once the

mackerel, by visual stimuli, approached each other. However, his data and those reported above on the behavior of blinded fishes would not tend to confirm this hypothesis.

Parr attributes the schooling reaction of mackerel to a simple automatic eye reflex rather than to a social instinct involving the entire school. The apparently senseless milling reaction is caused, he believes, when the school as a whole tries to make a turn of more than 180 degrees and is thus turned back on itself. This behavior pattern tends to emphasize the rather mechanical nature of the school.

Since the reaction of a mackerel to others of its kind is not to color it must be to form. However, form alone will not induce the schooling act if swimming movement is not normal. The fact that mackerel are evidently capable of detecting slight differences in movement would put the reaction of the fish on a slightly higher plane. Extensive heterotypic grouping experiments are planned which would tend to shed much light on the factors of response to various types of body form and movement. Further interesting data might be obtained by observing the reaction by an isolated mackerel to its mirror image. Following the work of Spooner (1931), the reflecting surface of the mirror could be broken by lengths of tape at definite intervals; in this way the reaction of the animal to body form which is identical with its own but not complete might be ascertained.

The condition of various types of fish schools and aggregations is summarized in a schematic diagram by Breder & Nigrelli (1935). Compared with other fishes possessing social tendencies, the schooling of mackerel is striking by virtue of its fixity. Nevertheless, the survival value of this mechanically highly integrated group is still not clear.

An interesting feature of the mackerel school is the spacing of the individuals in the group. The distance between the animals is more or less constant. A school may be greatly concentrated, however, by a sudden disturbance which produces a "fright" reaction — after being momentarily dispersed the fishes rush together in a compact mass which soon, however, returns to normal proportions. Parr (1927) states that when the fishes in a closely schooling group approach each other too closely, their images may become too large and the accompanying strenuous accommodation of the eyes may produce a negative response, thus regulating the spacing. Breder (1929) states the proposition that such fishes that depend on visual reactions for the formation of schools approach no closer to other objects than that distance at which they become clearly visible. This problem may be approached experimentally.

Whether the schooling habit is ontogenetically or phylogenetically acquired and whether the schooling or solitary state is the primitive one are important theoretical considerations. It is to be hoped that future investigation will shed some light on these problems.

#### SUMMARY.

1. Although larger groups are better integrated, two individuals suffice to begin the formation of a mackerel school.

2. Blinding, darkness, and visual contact experiments indicate that the schooling reaction of the mackerel is visually integrated.

3. Mackerel display no schooling reaction to others of the same species, living or dead, which move or are moved in a manner not completely normal.

4. As far as tested, response to body color plays no role in the schooling reaction.

5. Isolation for three weeks does not eliminate or reduce the schooling proclivity.

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#### EXPLANATION OF THE PLATE.

##### PLATE I.

- Fig. 1. A school of chub mackerel, *Pneumatophorus grex*, in an exhibition tank under fairly strong artificial light.
- Fig. 2. A flash-bulb photograph of the same school in total darkness—dispersed.
- Fig. 3. Mackerel milling in light in the deep red—650  $\mu$  to 700  $\mu$ .  
(The photographs include the upper four-fifths of the vertical depth and the central four-fifths of the length of the tank).

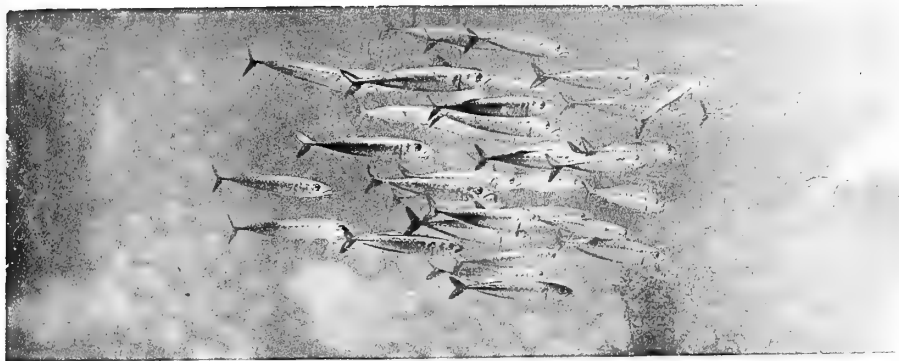


FIG. 1.



FIG. 2.

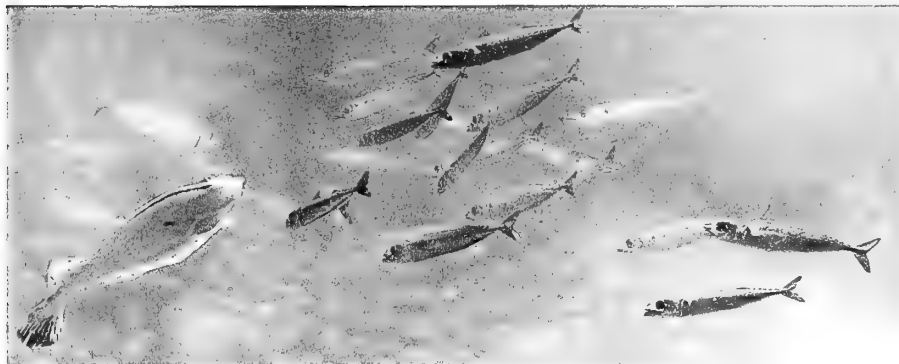


FIG. 3.

THE SCHOOLING BEHAVIOR OF MACKEREL: A PRELIMINARY EXPERIMENTAL ANALYSIS.



## 15.

## Food, Eggs and Young of the Carnivorous Snail *Euglandina rosea* (Férussac).

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&

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(Plate I).

The information contained herein is based on the observation of a single *Euglandina rosea* (Férussac) which was collected April 1, 1940, at Fort Myers, Florida, by Dr. William J. Hamilton, Jr., of Cornell University. On April 11 the snail was placed in a terrarium filled with humus and soil, at Ithaca, New York. Standing water was provided to keep the air in the container moist. The individual successfully survived until December 9, 1940, when accidental overheating caused its death. During the interval of 252 days observations concerning its food habits, eggs and young were carried out.

### FOOD OF *Euglandina*.

During this period of approximately 8 months the following New York land mollusks were placed in the terrarium with the carnivorous *Euglandina*: one *Mesomphix inornatus* (Say), two *Mesomphix cupreus* (Rafinesque), six *Anguispira alternata* (Say), and four newly hatched and two adults of *Triodopsis albolabris* (Say). Of these species only the *M. inornatus*, and the six *A. alternata* were devoured; the remaining snails were left untouched.

The *Euglandina* was observed during its process of feeding upon the *M. inornatus*. The predatory snail in approaching the *M. inornatus* lifted its head and anterior foot region in the air and moved them from side to side. This weaving back and forth continued for 60 seconds; during this time the greatly elongate lips were moved from side to side. Finally the *Euglandina* touched the body of the food snail, whereupon the latter contracted into its shell. The *Euglandina* then employed its anterior foot region to turn the *Mesomphix* shell over on its spire. This done, the predator entered the aperture

of the food snail's shell; the posterior foot region serving to hold the rest of the body firmly to the substratum. As soon as the *Euglandina* thrust its head into the *Mesomphix* shell aperture it began to feed with a piston-like motion, apparently forcing its head firmly against the soft parts of the prey so that the radula could obtain a firm purchase. The piston motion was accompanied by a lateral movement, indicating that the *Euglandina* was working from the columellar region outward, and then back again. Because of the thinness of the *M. inornatus* shell, the feeding could be observed without great difficulty. As the body of *Mesomphix* was gradually consumed the *Euglandina* worked further into the prey's shell, until its shell presented an effective block against further entrance. During the preliminary feeding the tentacle-like lips seemed to be thrust between the body of *Mesomphix* and its shell. Finally the columellar muscle of the *Mesomphix* was torn loose and the entire upper visceral mass was observed to disappear into the buccal cavity of the *Euglandina*. The feeding process took 40 minutes from the time of entrance until all of the body of *Mesomphix* had disappeared.

After the soft parts had been consumed the lips of the *Euglandina* were observed to move about the interior of the shell as though the animal was searching for food fragments which might have been overlooked. It seems likely that the sense of smell is well-developed in *Euglandina* and possibly serves this animal in locating food. Simpson's data (1901) indicates that the sense of smell is highly developed and used to locate food by *Triodopsis albolabris* (Say). He records this species moving 18

inches in order to feed on concealed lettuce. When the *Mesomphix* was placed in the terrarium with the carnivore, the latter was 10 inches removed and was fully contracted within its shell. In 3 minutes the *Euglandina* was active, and was moving toward the *Mesomphix*. A similar phenomenon was observed when one *A. alternata* was placed in the terrarium; the *Euglandina* was again contracted and motionless, 6 inches away from the *Anguispira*. In five minutes it became active and moved toward the food snail.

The six *A. alternata* and the one *M. inornatus* utilized as food were all turned over on their apices before they were devoured.

The following writers have discussed the snail food of *Euglandina rosea*. Baker (1903) reports *Euglandina* feeding upon the large Floridan pulmonate mollusks of the genera *Liguus* and *Orthalicus*. He observed that in some instances the voracious *Euglandina* will even bore a hole in the shell of the victim in order to reach the animal, instead of entering through the prey's aperture. Rogers (1908) states that *Euglandina* devours individuals of its own species and preys chiefly upon Helices. A. Binney (1851) reports *Euglandina* feeding on half-putrid remains of a *Helix*, and on Limacies which were confined together in the same container. He, too, writes that it preys on its own kind. W. G. Binney (1885) concerning the feeding habits of *E. rosea* states, "By its [the radula's] action the soft parts of its prey are rapidly rasped away or are forced in large morsels down the oesophagus. The animal has been seen to swallow entire the half-putrid remains of a *Helix*, and to attack *Limaces* confined in the same box with it, rasping off large portions of the integument, and in some instances destroying them. In one instance an individual attacked and devoured one of its own species, thrusting its long neck into the interior of the shell and removing all the viscera. I found many specimens of *Polygra volvoxis*, [*Polygra septemvolva* Say], in the stomach of individuals collected by me at Saint Augustine, Fla."

#### EGGS OF *Euglandina*.

In the second week of October the *Euglandina* deposited 22 eggs on the upper surface of the humus in the terrarium. This location was exposed to light, although more secretive places were available. Five of the eggs did not hatch. Because of periodic absence from the laboratory complete data on the incubation period were not obtained. The approximate incubation period was 60 to 68 days; the hatching period for individuals continued for 8 days after the first individual had emerged, 60 days after the egg had been laid.

The oval-oblong eggs were of nearly uniform size, measuring 4.25 mm. in length and from 3 to 3.25 mm. in width (Fig. 1). The egg shell is brittle and hard; no inner egg membrane is present. The egg shell is extremely rough, and is quite porous.

#### YOUNG OF *Euglandina*.

The young develop with their long axes coinciding with the long axis of the egg. The young break through the egg shell by means of the radula. A circular opening (Fig. 1) is first filed in the egg shell at the end surrounding the aperture of the young within. The initial hole is enlarged by use of the radula until approximately one-third of the egg shell is cut away (Fig. 2). This done, the young emerges, leaving an intact two-thirds of the shell behind. The exact amount of time required for the young to cut away enough shell to permit their escape was not observed. It is estimated, however, that with the young in question it was between 6 and 10 hours.

Little variation in size is shown in newly hatched young; of 15 that were measured the length varied .25 mm.; with the greatest length 4 mm., and the least 3.75 mm. Variation in width was also .25 mm.; the widest shell was 3 mm.; and the narrowest 2.75 mm. The largest young was 3.90 mm. in length and 2.90 mm. in width; the smallest was 3.75 mm. long and 2.75 mm. wide.

Each young has approximately two and one-fourth shell whorls upon hatching, as compared to the 6 to 8 whorls of fully mature shells. The aperture of the young is relatively large in proportion to the length of the shell, running approximately five-sevenths of the total shell length (Fig. 3). In the parent of these young the aperture was approximately equal to one-half of the total shell length. W. G. Binney (1885) concerning the length of young shells that he studied states, "In young individuals the spire forms but a small proportion of the shell, but in the old it often forms one-third of the length." A Binney (1851) comments on the shortness of the spire of young individuals, and at its enormous increase in mature shells. In an attempt to supply food for the young snails 4 small immature *T. albolabris* were placed within reach. Adult individuals of *A. alternata* were also available but individuals of neither species were touched. Apparently the lack of suitable animal food resulted in the death of the young 15 days after hatching.

#### NATURAL HABITAT OF *Euglandina*.

It should be understood that the observations included here were made in a habitat far from that in which *Euglandina rosea* is found. The data are, however, the most extensive to be reported on the eggs and young of *Euglandina*, and the photographic method



has not been used before to illustrate the eggs and young of this species.

The natural habitat is reported by W. G. Binney (1885) as follows, "The habits of this animal are somewhat aquatic. It is found on the sea islands of Georgia and around the keys and everglades of Florida, and in these situations the shell often attains the length of 4 inches; when found on the oyster hummocks and less humid localities it seldom exceeds 1 inch in length. Mr. Say found it in the marshes immediately behind the sand-hills of the coast. It is most readily found in the center of the clumps of coarse grass on these marshes." W. G. Binney (1885) lists the following distribution: Atlantic and Gulf States from North Carolina to Texas; Macon Springs, Georgia; Bibb County, Alabama; and Jackson, Mississippi. A. Binney (1851) indicates that it is common among the West Indian Islands. Pratt (1935) states that its distribution is from South Carolina to Texas.

#### ACKNOWLEDGMENTS.

The writers are indebted to Dr. William J. Hamilton, Jr., for supplying the *Euglan-*

*dina*. Credit is due Mr. Arthur Smith for taking the photographs of the eggs and the young.

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## EXPLANATION OF THE PLATE.

- Fig. 1. Egg of *Euglandina rosea*, showing initial opening cut by radula of young within its eggshell. Note porous and rough character of the shell.  $\times 21$ .
- Fig. 2. Egg of young three hours later, showing egg shell cut away, revealing the immature snail within.  $\times 23$ .
- Fig. 3. Newly hatched young which emerged approximately 6 hours after the initial opening had been made in the egg shell.  $\times 23$ .



FIG. 1.

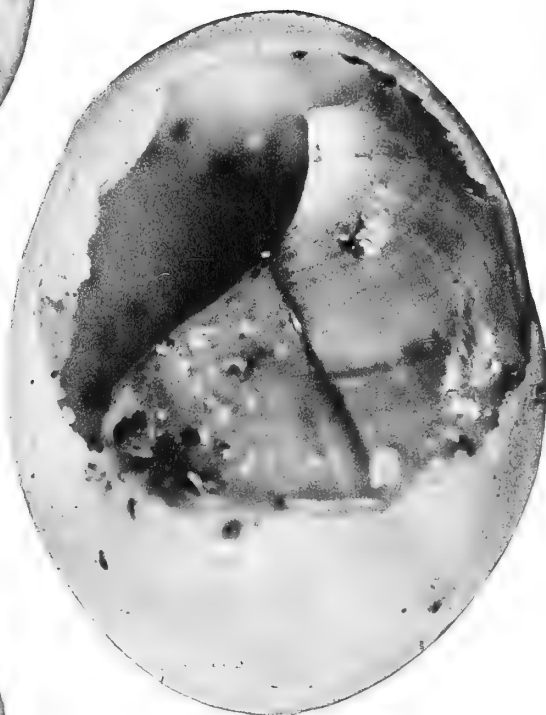


FIG. 2.

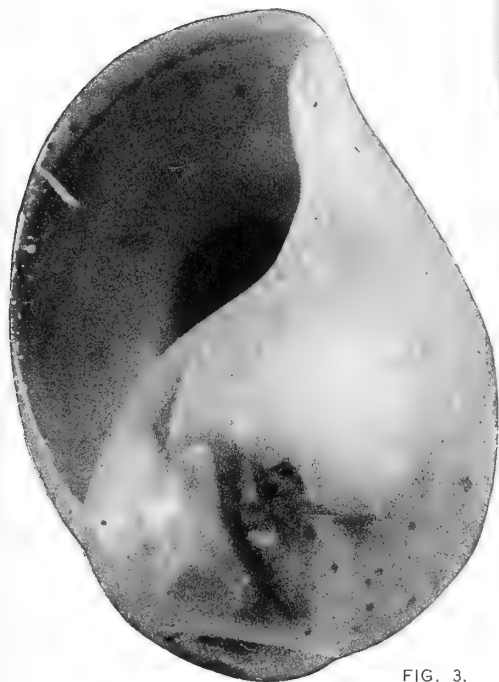


FIG. 3.

FOOD, EGGS AND YOUNG OF THE CARNIVOROUS SNAIL, *EUGLANDINA ROSEA* (FERUSSAC).



## 16.

# The Anatomy and Morphology of the Hypophysis of Several Species of Ovo-viviparous Poeciliids.\*

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(Plates I & II).

## INTRODUCTION.

The constantly growing knowledge of the endocrine glands makes increasingly apparent the complex physiological interrelationships of the pituitary. A great deal has been reported both on the morphology and the physiology of the pituitary but most of the investigations have been concerned with mammals where such structures as the mammary glands, corpora lutea and placenta introduce many complicating factors. It would seem possible to obtain some clarification of the many problems arising from these studies by an investigation of the pituitary in forms such as lower vertebrates in which the presence of fewer accessory structures makes the problem less complex.

A survey of the literature has shown a surprisingly incomplete knowledge of the pituitary of lower vertebrates, especially of teleost fishes (Stendell, 1914; deBeer, 1926; Charipper, 1937). This becomes especially apparent when one considers the various reports relating cell types in the anterior pituitary with the reproductive cycle in mammals (Rasmussen, 1921; Wolfe & Cleveland, 1933, 1933; Charipper & Haterius, 1932; Kirkman, 1937) as compared with the meager literature of a similar nature concerning the bony fishes. With regard to the latter group, Matthews (1936) has shown that the pituitary gland of *Fundulus* is not static but undergoes variations in cell type distribution which may be related to the different seasons of the year. Cardoso (1934), also working on an oviparous form, *Pimelodus clarias*, has shown a relation between gonad size and injection of hypophyseal suspensions. Houssay (1931), investigating the ovo-viviparous teleost, *Cnesterodon decemmaculatus*, described a relationship between ovulation and secretions of the pituitary. In addition, Rojas et al.

(1934) showed cyclic changes in the pituitary of *Jenynsia lineata*, another ovo-viviparous teleost. Further, the Teleostei as a group seem to offer many opportunities for descriptive investigations correlating variable hypophyseal histology and cytology to reproductive phenomena. In this group are a vast number of diminutive tropical fishes which present many evolutionary phases of reproduction from oviparity to true viviparity. This group of viviparous fishes are of particular interest because of the relatively short and usually regular reproductive cycle. These animals may be kept in large numbers in small aquaria, assuring a plentiful supply throughout the year. In addition, most of them can be bred readily so that animals in definite stages of the reproductive cycle may be easily obtained at all times.

With these facts in mind an investigation of the morphology and histology of the pituitaries of males and females of six species of ovo-viviparous teleosts was undertaken and forms the basis of the present report. The particular species examined were carefully chosen for availability and the ease with which they could be maintained and bred under laboratory conditions. In addition all these forms showed regular reproductive cycles of approximately thirty days. It is proposed that these descriptions constitute the beginning of what should prove to be an exhaustive survey and furnish a basis for future experimental investigations.

I wish to take this opportunity to express my deep appreciation to Dr. Harry A. Charipper for his generous and helpful assistance throughout the course of this investigation.

## MATERIALS AND METHODS.

The pituitaries of six different species of ovo-viviparous poeciliids, *Platypoecilus variatus*, *Xiphophorus helleri* (red, and

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green varieties), *Lebistes reticulatus*, *Limia tricolor*, *Mollienisia sphenops* and *Mollienisia latipinna* (black variety) were examined histologically. Specimens of *Mollienisia sphenops* and *latipinna* were obtained from a local dealer during the months of December, January and February. These were killed and fixed within two weeks of purchase. The other species were reared in aquaria at temperatures between 21 and 27 degrees centigrade and sacrificed at various times throughout the year.

Each fish was anaesthetized in ice water and the head severed immediately posterior to the gills and also cut just in front of the eyes. A fixing fluid composed of 18.5 cc. basic Zenker's to 1.5 cc. formalin gave the best results in about twenty hours. Following fixation, tissues were decalcified in phloroglucin 1½ hours and washed in running water 6 to 12 hours before dehydration and embedding.

Whole heads, or brain and pituitary, dissected free of all cartilage were then dehydrated and embedded in hard paraffin or tissue mat, after which they were cut at 5 micra in median sagittal, cross and horizontal sections.

The Masson technic was used almost exclusively. Timing and washing were standardized as carefully as possible in order to get comparable results on all six species. Earlier preparations were stained in Masson A ten minutes, rinsed in distilled water and destained in 1% phosphomolybdic acid 1¼ hours. They were then transferred directly to Masson C for thirty minutes, dipped in 95% alcohol, absolute alcohol, half and half absolute alcohol and xylol and then pure xylol, and finally mounted in Canada balsam. In later preparations the staining times were changed to three minutes in Masson A, thirty minutes in phosphomolybdic acid and 1 hour in Masson C. The latter timing gave better results although the staining affinities did not seem to be critically affected.

#### DESCRIPTION.

The pituitaries of the six species of poeciliids in this investigation show such striking similarities in morphology and histology that a single description will be made, using *Platypoecilus variatus* as the standard. The description will deal first with morphology and then with histology, under the headings cerebral portion (pars nervosa) and epithelial portion (pars anterior, intermedia, and uebergangsteil). Similarities and differences of the other species will then be considered separately.

#### I. *Platypoecilus variatus*

##### A. Morphology.

The pituitary is an ovoid gland, immediately behind the optic chiasma, attached to

the midventral floor of the diencephalon by a short hollow stalk. There is no sella turcica but the pituitary protrudes into a depression, the hypophyseal fenestra, closed ventrally by connective tissue (Pl. II, Fig. 12).

An extremely thin meninx primitiva extends from the brain down over the stalk and over the pituitary, carrying with it numerous small blood vessels.

There are four portions of the gland, distinguishable by staining reactions and cell types, namely, pars nervosa, anterior, intermedia and uebergangsteil (Pl. II, Fig. 7). No distinct septa separate the portions. The pars nervosa is a thickened and modified portion of the floor of the diencephalon, occupying the central dorsal region of the gland. The pars anterior, like a half sphere, has its posterior surface in contact with all the other parts of the gland. In its median dorsal portion, this contact is with the nervosa. Surrounding the nervosa completely ventrally and laterally, but only its ventral half anteriorly and posteriorly, is a convoluted layer of cells, the uebergangsteil, which contacts the posterior face of the pars anterior ventral and lateral to the nervosa. The pars intermedia is a shell-like portion surrounding the uebergangsteil completely ventrally, laterally and posteriorly, forming in the latter region the blunt posterior end of the gland. Anteriorly it is contiguous with the pars anterior lateral and ventral to the contact of the latter with the uebergangsteil.

#### B. Histology

##### 1. Cerebral Portion (Pars Nervosa)

The cerebral portion is composed of tissue from the floor of the diencephalon. It consists of masses of neuroglia cells and many interlacing fibres continuous through the infundibular stalk with the brain (Pl. I, Figs. 2, 4). The outer walls of the stalk are covered by a thin meninx primitiva whereas the inner walls are composed of ependyma cells which line the infundibular cavity.

The nuclei of ependyma and neuroglia cells are essentially similar, being rounded to ovoid and varying considerably in size. Each is surrounded by a well defined membrane and contains a centrally located, red-staining nucleolus and scattered pink to violet chromatin material. Nuclei are more abundant near the stalk and sparser in the central and more distal parts of the nervosa.

The cytoplasm of the ependyma cells is pale gray. Many irregular processes from them extend into the infundibular cavity. The cytoplasm of the neuroglia cells is indistinct and loosely fibrous, also staining a pale gray. Many tracts of fibres extend from the central portion of the nervosa into other parts of the gland as compact processes enclosing blood vessels which are thus distributed to the epithelial portions of the gland.

Penetration by these processes is especially heavy in the uebergangsteil and intermedia (Pl. I, Fig. 6; Pl. II, Fig. 7). In the dorsal posterior region of the nervosa the fibres run caudad through the low posterior end of the basket-shaped uebergangsteil and ramify among the cells of the pars intermedia (Pl. II, Fig. 7).

Colloid bodies of varying size and shape are characteristically present in the nervosa in varying amounts (Pl. I, Fig. 6; Pl. II, Figs. 7, 11). In the central region they are usually fairly large bodies but in the posterior region they are generally fine and granular. Their staining reaction varies in different glands from violet to pink, and both colors may be present in the same gland. In some cases large basophilic masses are filled with brilliant red-staining globules.

Free single cells, generally basophiles, are often found well within the nervosa. In some cases they appear normal but in others they show pycnotic nuclei and indistinctly outlined cytoplasm. The latter closely resemble many of the larger colloid masses.

## 2. Epithelial Portion

### a. Pars Anterior

The pars anterior is composed almost entirely of orange-red acidophiles, except for a tongue-like portion adjacent to the nervosa in the median dorsal portion of the gland. The acidophiles are closely packed, showing no definite arrangement into cords or tubules (Pl. II, Fig. 7). They vary in shape from rounded to ovoid to spindle shaped. Their size is also variable. The cytoplasm contains fine orange-red granules. The nuclei vary in size in relation to the size of the cells containing them. Their shapes range from spherical to elongate and their position may be central or apical. Within each nucleus are one or two red-staining spherical nucleoli surrounded by red-staining chromatin granules in a clear hyaloplasm. The tongue-like strip of tissue (Pl. I, Fig. 2) is a sheet several layers thick, roughly "V" shaped, which fits into the uebergangsteil with which it is continuous laterally and ventrally. Its posterior surface is in contact with the pars nervosa from which it is clearly separated by a membrane, and its anterior surface is in contact with the acidophilic part of the pars anterior. Here the delineation is less definite as many of the acidophiles penetrate the tongue-like portion irregularly. Many blood vessels pass through this sheet, enclosed within processes from the nervosa. The cells of this layer bordering the nervosa tend to be columnar while those within the sheet are poorly defined. The cytoplasm has a fleecy appearance and stains a pinkish-gray color. Nuclei are ovoid to spherical, containing a centrally located nucleolus and scattered granular chromatin, both of which stain

similarly to the cytoplasm.

### b. Pars Intermedia

The pars intermedia is composed entirely of basophiles. Its cytology is variable, the posterior part often showing a large number of basophiles, larger and more clearly defined than the cells of its middle portion, which closely resemble basophiles of the uebergangsteil. The cytoplasm of these larger ovoid to spherical cells ranges from violet to blue and appears homogeneous. Nuclei are roughly spherical, often having indentations which give them a vesicular appearance. They contain granular, faint pink-staining chromatin and a centrally located red-staining nucleolus. The rest of the intermedia cells are smaller and usually indistinctly outlined, their stainability varying from pale gray-blue to a deep blue. Small spherical vacuoles are often present. No special arrangement is apparent in these cells (Pl. I, Fig. 6; Pl. II, Figs. 7, 8). The nuclei are small and ovoid to spherical with well defined membranes in which is a granular chromophobic chromatin surrounding a centrally located red nucleolus. Nervosa processes enclosing blood vessels penetrate the middle region of the pars intermedia after passing through the uebergangsteil, while loose wavy masses of fibers penetrate the dorsal posterior portion directly (Pl. II, Fig. 7).

Besides varying in cell type, the pars intermedia varies in size. In some it is large while in others it is much reduced, forming a thin layer over the uebergangsteil and a small posterior part.

### C. Uebergangsteil

The uebergangsteil is the most changeable part of the gland, varying both as to size and as to proportions of its three cell types, basophiles, acidophiles and chromophobes (Pl. I, Fig. 6; Pl. II, Figs. 7, 8). Sometimes single cells or islets of cells lie free among the fibres of the pars nervosa.

The most common type of cell is a large polygonal or round deeply staining carmine red cell with well defined borders. The cytoplasm is filled with coarse carmine-colored granules. The nuclei are spherical to ovoid with a fine granular light red chromatin reticulum surrounding a centrally located brilliant red nucleolus. In some pituitaries these cells were present almost exclusively (Pl. I, Fig. 6). Other glands have an uebergangsteil which is heavily basophilic with a few scattered acidophiles and chromophobes. In such glands the stainable material of the acidophiles is often clumped and peripheral in location. The basophiles closely resemble the acidophiles in size and shape and their nuclei appear identical (Pl. II, Fig. 8). Their cytoplasm is optically homogeneous and varies in staining capacity

from pale gray-blue to deep blue. In some glands basophiles are present only in one or two spherical, centrally located masses which may be exclusively basophilic or may contain some acidophiles also. Chromophobes are smaller, poorly outlined and faintly pink-staining cells, more prevalent, if present at all, in the ventral region of the uebergangsteil. Their nuclei are similar to those of the chromophiles.

## II. *Xiphophorus helleri*.

The pituitary of *Xiphophorus* is typically deeper dorso-ventrally than that of *Platypoecilus variatus* and is more concave at its dorsal surface (Pl. I, Fig. 4).

Cell types of the four portions of the gland correspond to those described above with the exception that several small patches of basophiles are usually present in the pars anterior (Pl. I, Fig. 4). These have a small amount of fleecy, indistinctly outlined bluish-gray cytoplasm and nuclei with a coarsely granular, similarly colored chromatin reticulum. They resemble quite closely the cells of the tongue-like portion of the pars anterior.

Another difference from *Platypoecilus* is found in the arrangement of the cells of the uebergangsteil. In *Xiphophorus* cells of this region form a deep mass heavily penetrated by small curving fibrous tracts enclosing blood vessels, which, in median sagittal sections, appear to divide the tissue into rounded islands (Pl. I, Fig. 4). In *Platypoecilus* the uebergangsteil is a thinner, more convoluted layer through which the nervosa processes pass in a more direct manner.

## III. *Lebistes reticulatus*

The pituitary of *Lebistes reticulatus* is slightly more elongate and dorso-ventrally flattened than either of the preceding (Pl. I, Fig. 5; Pl. II, Fig. 10). Fewer nervosa processes penetrate the tongue-like portion of the pars anterior than is the case in *Platypoecilus variatus*. The uebergangsteil is more of a convoluted layer than in *Platypoecilus* (Pl. II, Fig. 10), and is heavily penetrated by nervosa processes with their blood vessels. One or two conspicuous masses of basophiles are characteristically present in the central region of the uebergangsteil.

In the pars intermedia of *Lebistes* a broad fibrous tract often reaches from the posterior end of the nervosa, postero-ventrally to the median ventral border of the gland. This is not shown in the figures of *Lebistes* but may be seen in Pl. I, Fig. 3, of *Mollienisia sphenops*, and Pl. II, Fig. 9, of *Limia tricolor*.

Cell types and arrangement are almost identical with those of *Platypoecilus*. However, patches of pale basophiles, similar to those of *Xiphophorus*, are occasionally pres-

ent in the pars anterior, especially in the Trinidad variety of *Lebistes*.

## IV. *Limia tricolor*

The pituitary of *Limia tricolor* is similar in shape to that of *Xiphophorus* (Pl. II, Fig. 9). The pars anterior is heavily penetrated by nervosa processes as in the case of *Platypoecilus*. A broad tract of nervosa fibres cut through the uebergangsteil and pars intermedia to the median ventral surface of the gland as in the case of *Lebistes*.

Cell types correspond to those in *Xiphophorus*, sparse groups of basophiles being characteristically present in the pars anterior.

## V. *Mollienisia sphenops*

The pituitary of *Mollienisia sphenops* is different in shape from all the others, being almost perfectly rounded, and flattened dorso-ventrally, (Pl. I, Fig. 3; Pl. II, Fig. 12). Like *Lebistes* and *Limia* it has a broad nervosa tract extending postero-ventrally through the uebergangsteil and pars intermedia to the median ventral surface of the gland. Occasional pale basophiles are found scattered in the pars anterior as in the case of *Xiphophorus*, and are also present along the nervosa processes entering the pars anterior.

The uebergangsteil is more highly convoluted than in *Platypoecilus* and *Lebistes*, and often a linear arrangement of carmine-colored acidophiles forms a border between the nervosa and basophiles and acidophiles of the deeper layer of the uebergangsteil.

## VI. *Mollienisia latipinna*

The pituitary of *Mollienisia latipinna* is most similar in shape to that of *Xiphophorus helleri* (Pl. I, Fig. 1). The extension of the infundibular cavity, the recessus hypophyseus, penetrates the gland more deeply than in any of the other species. Many nervosa processes with their blood vessels penetrate the tongue-like portion of the pars anterior to be distributed throughout the basophilic part of the pars anterior. Along these processes, and scattered in small groups throughout the mass of acidophiles, are pale basophiles, a condition similar to that found in *Mollienisia sphenops*.

## DISCUSSION.

### I. Anatomy

Pituitary morphology and histology are fundamentally similar in the six species of poeciliids examined. The glands most closely resemble those of the egg laying poeciliid, *Fundulus*, and the ovo-viviparous poeciliid, *Jenynsia lineata*, as described by Scruggs (1939) and Rojas et al. (1934) respectively.

The infundibular stalk is highly variable among teleosts, being almost non-existent in *Mormyrus* (Stendell, 1914), the pituitary



being held close to the brain, and short in *Fundulus* (Matthews, 1936) and *Carassius auratus* (Bell, 1937, 1938; Levenstein, 1939; Scruggs, 1939). In *Lophius piscatorius* (de Beer, 1926) the stalk reaches its highest development, extending anteriorly for a considerable distance. It may be solid as in *Carassius* or hollow as in *Pungitius* (Scruggs, 1939) and in the poeciliids described here.

No structure comparable to a sella turcica is present in the teleosts. In *Fundulus* (Matthews, 1936) and *Carassius* (Bell, 1938; Levenstein, 1939) the pituitary is protected by the parasphenoid bone. The poeciliid crania of this investigation differ from the above, being of the platybasic type as described by Kingsley (1936). The cranium floor is composed of calcified connective tissue which spreads out laterally over the trabeculae cranii. The pituitary projects ventrally into the hypophyseal fenestra, a depression in the floor of the cranium.

#### A. Pars Nervosa

The pars nervosa protrudes into the gland at different angles in various teleosts. In *Carassius* (Bell, 1938; Levenstein, 1939) and in *Cyprinus* (Scruggs, 1939) the gland is tilted forward and the nervosa runs anteriorly. In *Ameiurus nebulosus* (Scruggs, 1939) the pituitary is tilted backward and the nervosa runs posteriorly. In the poeciliids investigated here the pituitary is directly beneath the infundibular stalk and the nervosa is directed vertically downward.

A recessus hypophyseus, representing an extension of the infundibular cavity into the nervosa, is present in *Jenynsia* (Rojas et al., 1934), *Fundulus* (Matthews, 1936), and in the poeciliids of this investigation. It is lacking in some teleosts, as *Carassius* (Bell, 1938; Levenstein, 1939) and *Ameiurus* (Scruggs, 1939).

There is also much variation in the number of nervosa processes given off and in their penetration of the various portions of the gland. In *Pseudopleuronectes americanus* and *Cyprinus carpio* (Scruggs, 1939) the nervosa processes are limited exclusively to the pars intermedia; in *Fundulus*, to pars intermedia and uebergangsteil; in *Carassius*, *Jenynsia* and the poeciliids of this report, the nervosa processes go to all parts of the pituitary.

#### B. Pars Anterior

The proportions, contacts and positions occupied by the various portions of the pituitary in different teleosts are highly variable. In *Carassius* (Bell, 1938; Levenstein, 1939; Scruggs, 1939) and in *Cyprinus carpio* (Stendell, 1914; Scruggs, 1939) the pars anterior is small, dorsal in position and makes contact with the uebergangsteil mostly and the nervosa only in a limited

area. In *Notemigonus* (Scruggs, 1939) it is large and anterior in position, making contact with the uebergangsteil and the main portion of the nervosa. In *Ameiurus nebulosus* the pars anterior is small. It is anterior and ventral in position, again making contact with uebergangsteil and nervosa (Scruggs, 1939). In the fishes of the investigation the pars anterior is very large, anterior in position, and touches nervosa, uebergangsteil and pars intermedia. The variations, however, are more apparent than real, being due in large part to a tilting of the pituitary either backward or forward.

A pars anterior has been reported for all teleosts examined except *Esox niger* (Scruggs, 1939) and *Fundulus* (Matthews, 1936). However, in his 1937 paper Matthews decided that the anterior portion of the pituitary, previously called the uebergangsteil, was actually the pars anterior. This was substantiated by Scruggs (1939) on the basis of staining reactions. In the case of *Esox niger* Scruggs found no portion taking a stain like that of the pars anterior of other teleosts; Stendell (1914), however, describes a small pars anterior for *Esox lucius*.

#### C. Pars Intermedia

The pars intermedia of teleosts has usually been identified by its close relationship with the pars nervosa. Stendell (1914) shows an intimate relationship of the two parts in the primitive *Mormyrus*, while in the higher teleost, *Esox lucius*, the pars intermedia is more posterior in position and retains its association with the nervosa by means of nervosa processes extending out into it. It extends forward ventrally, reaching or nearly reaching the posterior end of the pars anterior, thus surrounding the uebergangsteil ventrally. While Matthews (1937) divides the pituitary of *Fundulus* into only two epithelial portions, a pars anterior and a pars intermedia, Scruggs (1939) shows that the latter portion may be differentiated, by the Dawson & Friedgood (1938) method, into two portions comparable to the pars intermedia and the uebergangsteil of other teleosts. The pituitary of the poeciliids of this investigation compare with that of *Fundulus* as found by Scruggs, having an uebergangsteil adjacent to the pars nervosa and a pars intermedia which surrounds it laterally, ventrally and posteriorly. Connection with the nervosa is direct posteriorly and by means of nervosa processes extending through the uebergangsteil centrally and anteriorly.

#### D. Uebergangsteil

The uebergangsteil is present in some cyclostomes and all teleosts. It is highly variable in the latter, the simplest condition being found in *Mormyrus* where the

pars anterior, uebergangsteil and pars intermedia are arranged in linear order with no distinct boundaries between them. In *Gasterosteus* (Bock, 1928) connective tissue septa separate the parts. In *Carassius auratus* (Bell, 1938) the uebergangsteil is very large, bordered by connective tissue, and forms most of the anterior part of the gland. In *Esox niger* (Scruggs, 1939) no pars anterior is reported and the uebergangsteil occupies the antero-dorsal region of the gland, being in size, shape and location similar to the pars anterior of *Carassius auratus*. The uebergangsteil of the poeciliids investigated here has no connective tissue septa, is moderately large, and as in most teleosts, lies between the pars anterior and the pars intermedia, a portion of the latter extending over it, however, in the middle region of the gland. It is highly variable in individuals of the same species, being a large deep layer in some, a thinner layer in others. In *Lebistes*, *Platypoecilus* and *Mollienisia sphenops* it tends to be highly convoluted while in the other species examined it is a thicker, less folded layer.

## II. Histology

### A. Pars Nervosa

Stendell (1914) described the nervosa most completely. It is composed chiefly of neuroglia cells. The infundibular cavity and recessus hypophyseus are lined with primitive ependyma cells having protoplasmic extensions both basally and distally. Bock (1928) confirms these findings in *Gasterosteus*. Through the neuroglia network Stendell describes lymph tracts, blood vessels and connective tissue. Stolon-like nervosa processes extend to all parts of the gland. He interprets the structure of the nervosa as providing the means of absorption of pars intermedia secretions by way of lymph and blood vessels. Colloid masses among nervosa fibres, he believes represent secretion of degenerating pars intermedia cells. Collin (1924), in mammals, Florentin & Weiss (1931), Florentin (1934) and Rojas et al. (1934), in teleosts, hold the same theory of secretion and absorption. The structure of the pars nervosa of the poeciliids investigated here confirms that of the above authors. Nervosa processes ramify throughout all portions of the pituitary, especially the pars intermedia. Colloid masses of varying size and amount are present in the nervosa and pars intermedia. Matthews (1936), Levenstein (1939), Scruggs (1939) and others call attention to masses of colloid in the nervosa. Stendell (1914) also notes many free cells of the pars intermedia lying in the nervosa and believes that they degenerate into colloid. In the present work a number of free cells were seen lying in the nervosa, some appearing degenerate and closely resembling colloid masses.

### B. Pars Anterior

The pars anterior of teleosts differs greatly from that of other vertebrates, consisting almost entirely of acidophiles, with sometimes a scattering of basophiles. Entirely basophilic pars anteriors have been reported in the eel, *Cyprinus*, *Esox lucius* and in *Carassius* by Tilney (1911), Stendell (1914) and Bell (1938). However, modern technics have shown these same portions to be predominantly acidophilic (Florentin & Weiss, 1931; Scruggs, 1939; Levenstein, 1939). These discrepancies thus appear to be due to differences in staining technics.

In the present work the pars anterior is almost entirely acidophilic. Occasional single or small groups of pale basophiles may be present, especially in *Xiphophorus*, *Limia* and the *Mollienisia*s. Their scarcity precludes any great physiological significance. An additional type of cell, an orange acidophile, is described in some species by Scruggs, using the Dawson & Friedgood technic. These are difficult to interpret since in some species they are the predominant or exclusive type of cell present in the pars anterior while in others a few are present among a background of carmine-staining cells. Also similar orange cells are described in the pars intermedia of some species.

The arrangement of pars anterior cells differs greatly in the various groups of teleosts, varying from a compact condition with no special arrangement as found in the poeciliids in this report to a tubular distribution in which the cells are arranged around lumina, as in the eel (Tilney, 1911) and in the Salmonidae (Scruggs, 1939). An intermediate condition, where the cells are arranged in solid cords, is seen in the cod (Herring, 1908). In those forms in which cord or tubule arrangement is present the cords or tubules are separated from one another by connective tissue septa. Such separation is difficult to discern, or absent in the compact type of gland.

A pale basophilic or chromophobic tongue-like portion of the pars anterior has received little attention; Bock (1928) reports it in *Gasterosteus* and Scruggs refers to it briefly in the Salmonidae, *Fundulus* and *Pungitius*. This portion is present in all the Poeciliidae investigated in the present report, occupying a position in the dorsal half of the gland, between the acidophilic part of the pars anterior and the pars nervosa. It is a layer several cells in thickness, the cells adjacent to the pars nervosa being ependyma-like, oriented with their long axes perpendicular to their contact with the nervosa.

### C. Pars Intermedia

Most of the recent work on teleost pituitaries shows the pars intermedia to be composed almost entirely of small pale-staining

basophiles. Scruggs (1939), using the Dawson & Friedgood technic, also found a varying number of orange cells. In *Esox*, Scruggs describes basophiles, orange cells and carmine cells; in *Fundulus*, basophiles, chromophobes and orange cells. Matthews (1936) describes acidophiles of the pars intermedia lining the nervosa processes. These cells, however, seem to belong to the uebergangsteil as described by Scruggs in the same species, rather than to the pars intermedia. The poeciliids investigated in the present report closely resemble *Fundulus* in pituitary structure. In these the pars intermedia, with the Masson stain, is entirely basophilic. The uebergangsteil lies between part of the intermedia and the nervosa, and deep red cells of the uebergangsteil often line the nervosa processes.

The arrangement of cells in the pars intermedia is generally agreed to by all investigators. In *Anguilla* and *Esox* (Stendell, 1914) polygonal cells form a compact stratum traversed by many nervosa processes. Bordering the nervosa processes the cells become cuboidal to columnar, forming an epithelium. Bell (1938) describes the cells of the pars intermedia of *Carassius* as ovoid or polygonal but forming an epithelial layer about the nervosa processes. Scruggs describes the intermedia cells of *Carassius* as indistinctly outlined. In the present work the pars intermedia shows a compact arrangement with polygonal or indistinctly outlined cells. An epithelial arrangement may occasionally be found adjacent to nervosa processes.

The pars intermedia varies both in structure and in the proportion of the gland which it occupies. Rojas et al. describe the disappearance of typical cells in the posterior portion and the appearance of colloid droplets in this location. The same condition is noted in the pars intermedia of the poeciliids investigated here. The dorsal portion of the intermedia is sometimes filled with small colloid droplets and few typical cells are present. Herring (1908) was the first to note such colloid in his work on the cod, and since then Stendell (1914) and many others have called attention to its presence. Scruggs (1939) reports a decrease in the size of the pars intermedia of *Fundulus* in January as compared with June. The pars intermedia of the poeciliids investigated here shows considerable variation in the proportion of the gland which it forms. In some cases a portion of its territory is occupied by large basophiles which appear to belong to the uebergangsteil.

#### D. Uebergangsteil

The uebergangsteil is composed of acidophiles and basophiles in the eel and in *Mormyrus*, acidophiles predominating in the former and basophiles in the latter (Sten-

dell, 1914). In the stickleback (Bock, 1928) chromophobes and a few basophiles are present. Scruggs (1939) finds no acidophiles in the uebergangsteil of the eel, only basophiles and chromophobes being present. In most of the teleosts examined by him, he reports deep-staining acidophiles and basophiles, and chromophobes. The poeciliids examined here have the three characteristic cell types.

Uebergangsteil cells may form a compact mass with acidophiles and basophiles scattered in groups (Bell, 1937, 1938; Charipper, 1937; Levenstein, 1939; Scruggs, 1939) or a folded epithelial configuration as seen in Scruggs' figures of the Centrarchidae and Poeciliidae. A similar condition is seen in the figures of Matthews (1936), Rojas et al. (1934) and in the poeciliids of this investigation.

Cell type proportions are highly variable in the uebergangsteil of any single species. Bock (1928), Rojas et al. (1934), Matthews (1936) and Scruggs (1939) all call attention to changes in cell types. Matthews finds seasonal changes in the proportionate number of acidophiles and basophiles of *Fundulus*. A particular type of basophile is present in the posterior part of the pars intermedia only at certain times of the year. Scruggs also reports seasonal changes in the *Fundulus* pituitary and describes the migration of large deep-staining basophiles which invade the posterior part of the pars intermedia. In this investigation, large basophiles are present in many specimens in the posterior part of the pars intermedia, similar to those of the uebergangsteil. Also great variability is manifested in percentage of basophiles and acidophiles in different individuals, the uebergangsteil of some being almost entirely basophilic, others almost entirely acidophilic, still others having varying proportions of each. These variations are suggestive of a regulated cyclic variation which may be related to the reproductive cycle. However, cell counts failed to establish any definite relationship between stages of the reproductive and percentage of cell types.

#### E. Colloid

Herring (1908) first called attention to colloid in the cod pituitary. Stendell (1914) emphasized the functional relationship between nervosa and pars intermedia and postulates two methods of secretion by the intermedia, one by release of minute colloid droplets which are absorbed by the nervosa processes. In the second, intermedia cells wander into the nervosa and disintegrate, forming secretory material which is absorbed by the nervosa. Rojas et al. (1934) and Florentin (1934) likewise describe holocrine secretion in teleost pituitaries. Rojas states that cells of the posterior part of the pars intermedia degenerate and only colloid is left in their place. Matthews (1936) de-

scribes acidophilic colloid in the nervosa which closely resembles the secretory inclusions of the acidophiles of the pars "intermedia" as described by him. In the poeciliids investigated here the posterior portion of the pars intermedia is highly colloidal in many specimens and few cells are present. In others the region is cellular and has little or no colloid. Also single cells or small groups of cells from the uebergangsteil are sometimes present in the nervosa, many of them apparently in the process of disintegration and closely resembling some of the colloid masses. Thus both types of secretion as interpreted by Stendell (1914) are confirmed in this report.

#### F. Blood Supply

Bock (1928) and Bell (1938) describe poor vascularization in the pituitaries of *Gasterosteus* and *Carassius* respectively. On the other hand, a heavy vascular supply is described in the eel (Tilney, 1911) and *Cyprinus* and *Esox* (Stendell, 1914). The poeciliids investigated here most closely resemble the eel in vascularity. Large vessels in the nervosa radiate outward in all directions within the nervosa processes, and penetrate all parts of the gland.

#### G. Homologies

Establishment of homologies of the parts of the teleost pituitary with those of mammals is desirable as a prelude to experimental work. Stendell (1914), Charipper (1937), Bell (1938) and Levenstein (1939) homologize the teleost uebergangsteil with the mammalian pars anterior. Levenstein shows two types of chromophobes in the uebergangsteil having Golgi corresponding to those of the acidophiles and basophiles of this portion. This compares with the findings of Addison (1916), Atwell (1929), Severinghaus (1933) and Kirkman (1937) in mammals. The present work shows three types of cells in the teleost uebergangsteil similar to those in the mammalian pars anterior. The pars intermedia of mammals and teleosts occupies a similar position and is almost exclusively basophilic.

The pars anterior of teleosts is interpreted by Bock as a portion unrelated to the pars anterior of higher vertebrates. Charipper (1937) and Bell (1938) compare it with the pars tuberalis of higher forms on the basis of location, cord-like arrangement of cells and basophilic staining reaction. Scruggs (1939), using the Dawson & Friedgood technic, finds the teleost pars anterior to be acidophilic, however, while the pars tuberalis of mammals is chromophobic with the same technic. In the present investigation a tongue-like portion of the pars anterior, occupying a position along the dorso-anterior surface of the nervosa, close to the infundibular stalk and brain,

takes a pale basophilic or chromophobic stain. Bock (1928) and Scruggs (1939) describe a similar portion in several teleosts. This portion seems to compare more favorably with the pars tuberalis of higher forms. If this be the case, then the rest of the pars anterior can be considered only as a separate structure characteristic of teleosts and of some cyclostomes.

#### SUMMARY AND CONCLUSIONS

1. The pituitaries of the six species of ovoviparous poeciliids conform, in the presence and general disposition of epithelial and nervous portions, with the structure reported for other teleost fishes. The four portions are the pars anterior, pars intermedia, uebergangsteil and pars nervosa.
2. Boundaries between the parts are established by abrupt changes in cell type rather than by connective tissue septa.
3. The pars nervosa consists of a solid mass of fibrous tissue and neuroglia cells. It occupies the dorsal and central portion of the pituitary gland and sends solid root-like processes to all the epithelial portions. Within the nervosa are varying amounts of colloid, usually violet-colored, large, amorphous masses and some finer acidophilic granules.
4. The pars anterior is composed almost entirely of small orange-red acidophiles which show no special arrangement into cords or nests. A tongue-like strip of faintly basophilic or chromophobic cells separates the acidophilic portion from the pars nervosa throughout the dorsal half of the gland.
5. Only occasional single or small groups of basophiles are present in the pars anterior of *Xiphophorus helleri*, *Limia tricolor*, *Mollenisia latipinna* and *Mollenisia sphenops*, and in a few *Lebistes*.
6. The pars intermedia consists of small faintly-staining basophiles showing no special arrangement. The posterior region is less cellular and more heavily penetrated by fibres from the nervosa and takes a violet color with the Masson stain. The middle portion is heavily cellular and stains light blue. Many small vacuoles but little or no colloid are present in this region.
7. The uebergangsteil is a thick layer of cells surrounding the pars nervosa completely laterally but only on its ventral half anteriorly and posteriorly. It may form a highly convoluted layer typical of *Lebistes* and *Platypoecilus variatus*, or a thicker, less folded layer as in *Xiphophorus helleri*. In all cases many strands of the nervosa penetrate it to reach the middle portion of the pars intermedia. Large granular acidophiles, large and more homogeneous basophiles

and occasional chromophobes constitute the cellular population of this region.

8. There appears to be a regulated variation of the pars intermedia and the uebergangsteil in which the proportions occupied by the two parts varies inversely. Not only do the proportions of the two parts change but also the ratio of basophiles and acidophiles in the uebergangsteil changes. No correlation was established, however, between these changes and stages of the reproductive cycle.
9. The pars anterior, intermedia and nervosa have an abundant blood supply. The uebergangsteil has no direct blood supply, but it is penetrated in many places by strands of the nervosa tissue, each of which ensheathes a blood vessel. The many foldings of the uebergangsteil layer bring most of the epithelial tissue in close contact with the blood vessels. In cases where the uebergangsteil is not convoluted the nervosa processes with their blood vessels show heavy anastomoses with each other, thus dividing the epithelium into many patches or islands bordered by blood vessels.

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## EXPLANATION OF THE PLATE.

All material illustrated has been fixed with a modified Helly's fluid, stained with the Masson stain, and cut at 5 micra (except Fig. 3 which was cut at 7 micra).

## PLATE I.

- Fig. 1. Median sagittal section through the infundibular stalk of a female *Mollienisia latipinna*, showing the recessus hypophyseus, nervosa processes entering the pars anterior and other portions of the gland.  $\times 140$ .
- Fig. 2. Median sagittal section through the pituitary of *Platypoecilus variatus* showing pars nervosa and part of pars anterior. Neuroglia cells and fibres are visible in the pars nervosa. The tongue-like portion of the pars anterior is clearly visible.  $\times 610$ .
- Fig. 3. Median sagittal section through the infundibular stalk of *Mollienisia sphenops* showing nervosa tract descending from the posterior region of the pars nervosa to the ventral border of the gland. A patch of basophiles is present in the pars anterior, adjacent to a nervosa process. The convoluted arrangement of the uebergangsteil is apparent. Colloid is abundant both in the pars nervosa and in the posterior region of the pars intermedia.  $\times 250$ .
- Fig. 4. Median sagittal section through the infundibular stalk of *Xiphophorus helleri* showing the four portions of the gland. Small gray patches of basophiles and the gray tongue-like portion can be seen in the pars anterior. Also, small fibrous tracts carrying blood-vessels can be seen penetrating the uebergangsteil.  $\times 175$ .
- Fig. 5. Median sagittal section through the infundibular stalk of the pituitary of a female *Lebistes reticulatus* showing the different portions of the gland. The pituitary is more elongate and dorso-ventrally flattened than in the other species.  $\times 300$ .
- Fig. 6. Cross section through the infundibular stalk of *Platypoecilus variatus* showing the sharp demarcation of the uebergangsteil (dark staining cells) from the middle region of the pars

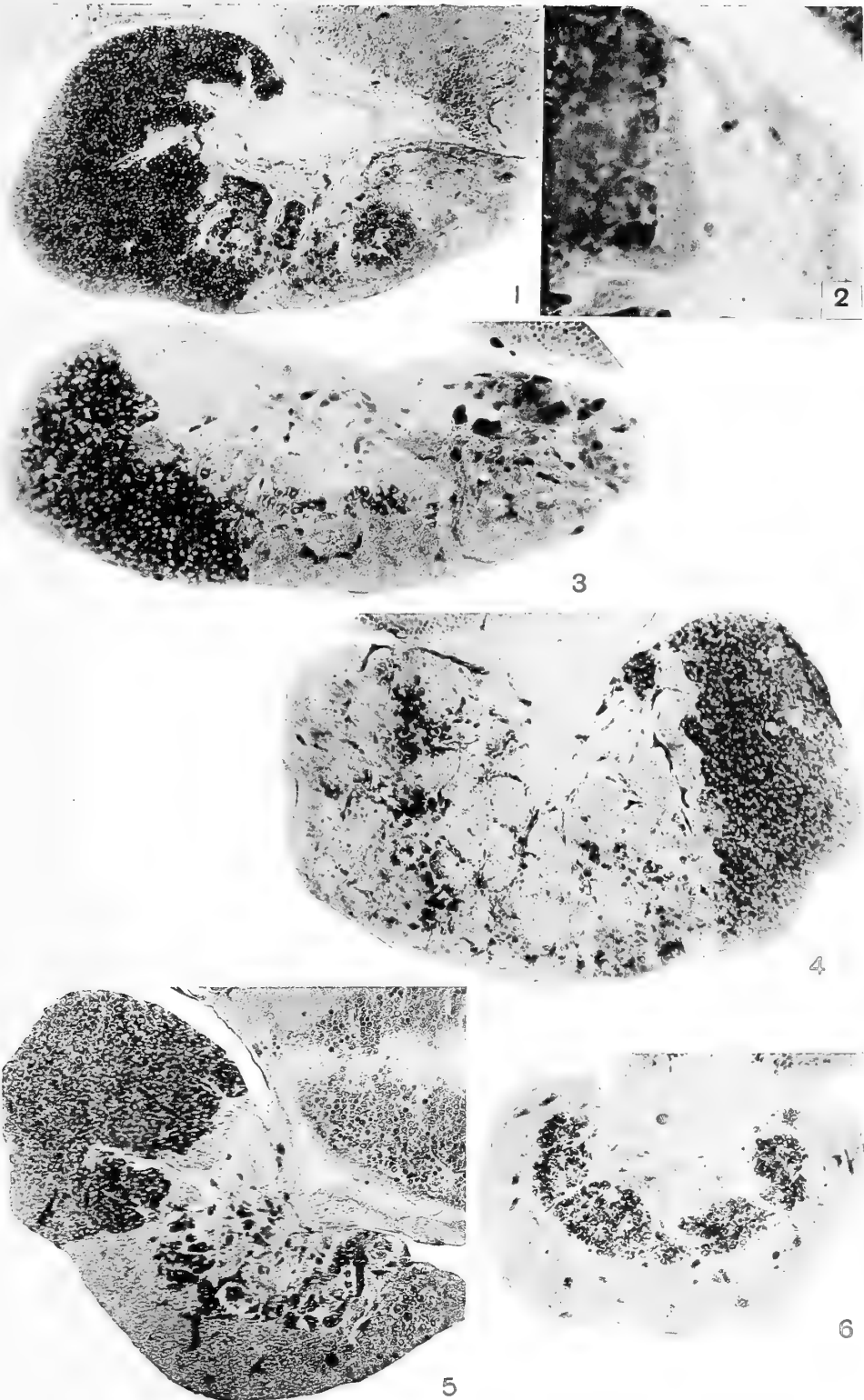
intermedia. Colloid bodies and nervosa processes can be seen in the nervosa.  $\times 160$ .

## PLATE II.

- Fig. 7. Median sagittal section through the infundibular stalk of a male *Platypoecilus variatus*, the four portions of the gland. The pars anterior is composed almost completely of dark-staining acidophiles. In the pars nervosa colloid bodies are seen among the neuroglia cells and fibres. The uebergangsteil is composed of basophiles and acidophiles, some of which invade the pars intermedia ventrally.  $\times 220$ .
- Fig. 8. Median sagittal section through the pituitary of *Platypoecilus variatus*, showing the large acidophiles and basophiles of the uebergangsteil. Below them are the small basophiles of the pars intermedia.  $\times 900$ .
- Fig. 9. Median sagittal section through the pituitary gland of *Limia tricolor*. A tract of pars nervosa fibres can be seen penetrating to the ventral border of the gland. Many colloid masses are present in this tract and in the dorsal posterior region.  $\times 240$ .
- Fig. 10. Cross-section through the infundibular cavity of the pituitary of *Lebistes reticulatus*, showing the highly convoluted uebergangsteil.  $\times 300$ .
- Fig. 11. Cross-section through the mid-region of the pituitary of *Platypoecilus variatus*, showing the pars nervosa surrounded by the uebergangsteil. Colloid bodies are prominent in the pars nervosa. Numerous blood vessels carried in nervosa processes penetrate the uebergangsteil.  $\times 460$ .
- Fig. 12. Cross-section through the infundibular stalk of the pituitary of *Mollienisia sphenops*, showing a part of the pars anterior at the right. Beneath the gland may be seen the hypophyseal fenestra.  $\times 160$ .

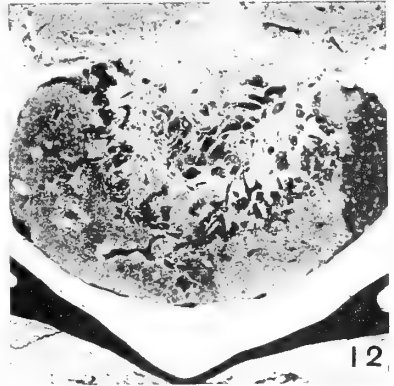
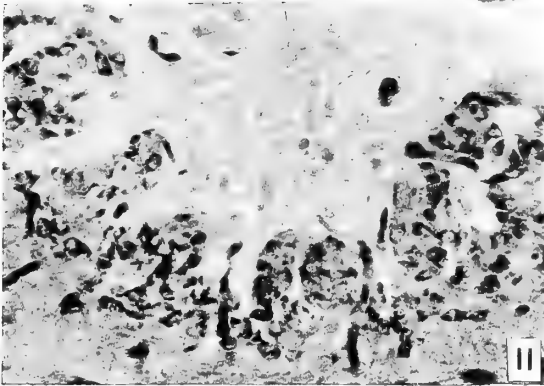
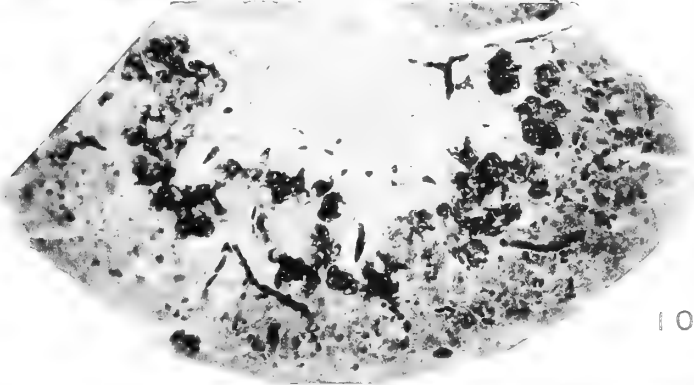
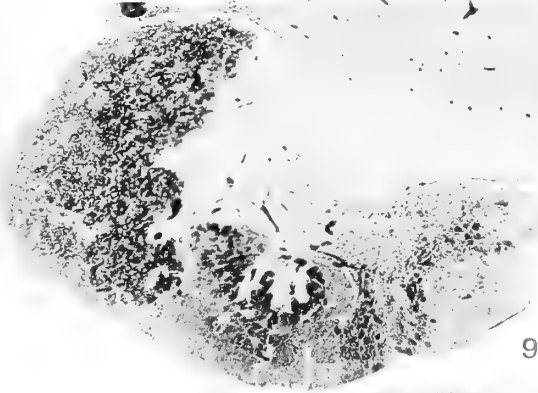
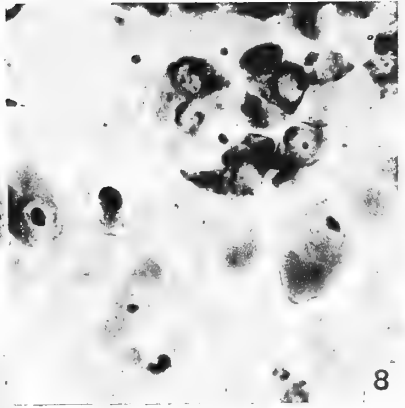
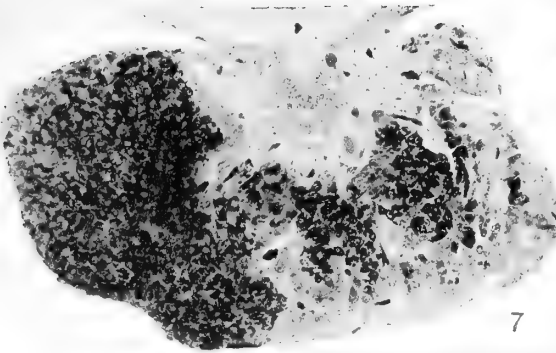






THE ANATOMY AND MORPHOLOGY OF THE HYPOPHYSIS OF SEVERAL SPECIES  
OF OVO-VIVIPAROUS POECILIIDS.





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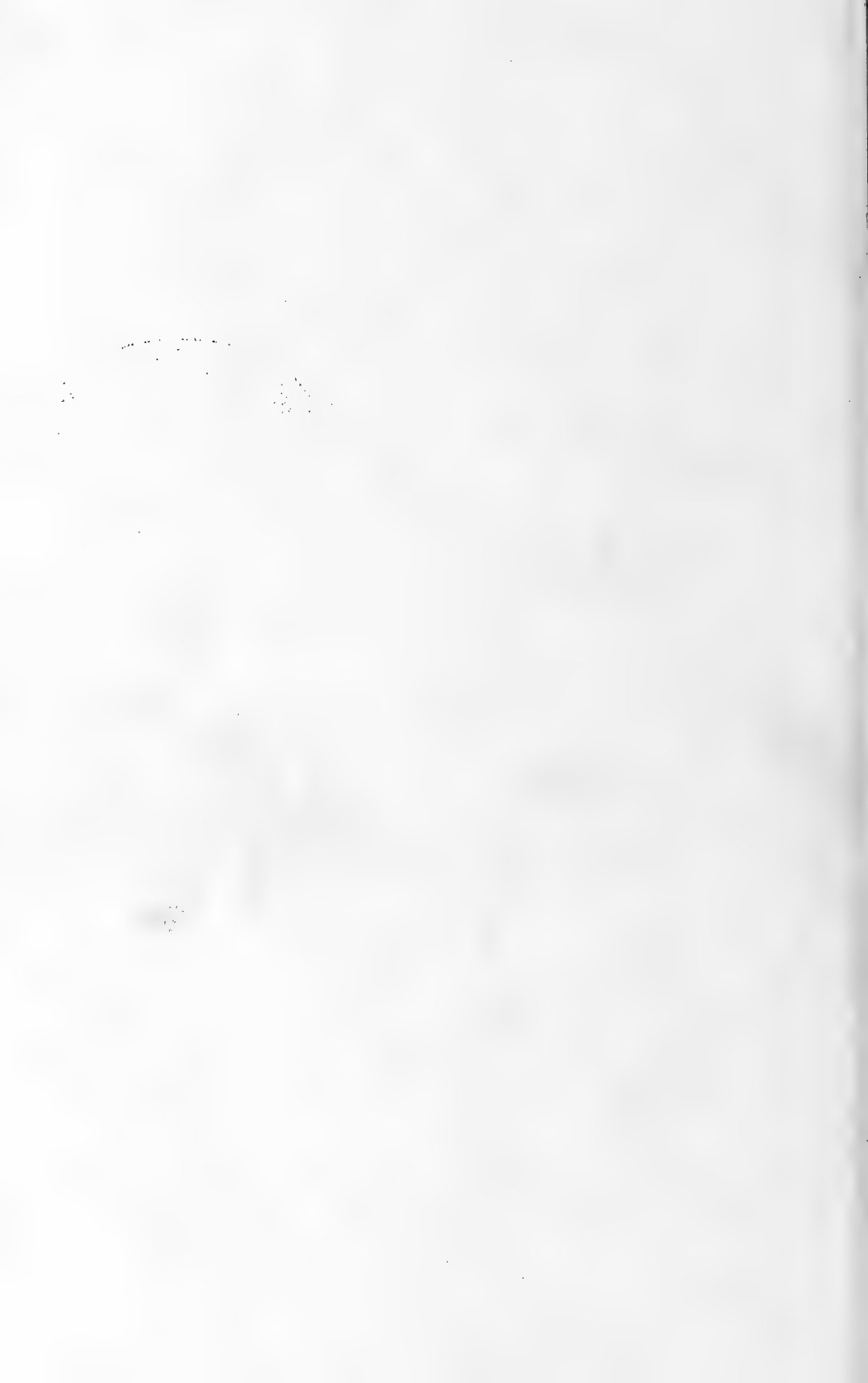
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## 17.

# The Synonymy of the Garter Snakes (*Thamnophis*), with Notes on Mexican and Central American Species.

HOBART M. SMITH.

The accumulation in recent years of relatively large series of garter snakes from Mexico and Central America has made possible a more satisfactory definition of the various species occurring in that area than was possible when Ruthven completed his study of the genus in 1908 (*Bull. U. S. Nat. Mus.*, no. 61). The redefinition of them attempted here has made necessary a re-examination of types and type descriptions, and a number of surprising facts have come to light. While the allocation of names was undertaken chiefly to clarify the synonymy of Mexican garter snakes, all names which have been proposed in or subsequently referred to the genus *Thamnophis* have been allocated. Since these are not available in any one place, they are listed below with original place of description, type locality and present status. The discussions which follow this list concern only those species occurring in mainland Mexico and Central America. Specimen numbers, unless otherwise indicated, are from the U. S. National Museum.

I am much indebted to Dr. E. H. Taylor for numerous courtesies, specimens and advice; and to Dr. K. P. Schmidt for the opportunity to study material in Field Museum of Natural History.

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*Baronis Müller*, *Tropidonotus*. Troschel, in Müller, *Reisen Ver. Staat, Can., Mex.*, 1865, pp. 610-611. Mexico. = *T. melanogaster canescens*. (Not binomial, therefore not available.)

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- flavilabris*, *Eutaenia*. Cope, *Proc. Acad. Nat. Sci. Phila.*, 1866, p. 306. Tableland or southern mountains of Mexico. = *T. macrostemma macrostemma*.
- fulvus*, *Eutaenia cyrtopsis*. Bocourt, *Miss. Sci. Mex.*, Rept., 1893, pp. 777-8, pl. 62, fig. 2. Alta Verapaz, Guatemala. = *T. sumichrasti fulvus*.
- gigas*, *Thamnophis ordinoides*. Fitch, *Univ. Calif. Publ. Zool.*, vol. 44, pp. 69-73, pl. 5, fig. 7, pl. 7, fig. 7. Gadwall, Merced Co., California.
- glaphyros*, *Tropidonotus*. Jan, *Elenco Sist. Ofidi*, 1863, p. 70. North America. = *T. radix*.
- godmani*, *Tropidonotus*. Gunther, *Biol. Centr. Amer.*, Rept., 1894, p. 133. Omilteme, Guerrero. = *T. scalaris godmani*.
- graminea*, *Eutaenia sirtalis*. Cope, *Proc. U. S. Nat. Mus.*, vol. 11, 1889, p. 399. Brookville, Indiana. = *T. sirtalis sirtalis*.
- halophilus*, *Thamnophis*. Taylor, *Herpetologica*, vol. 1, 1939, pp. 183-187, pl. 19, text-fig. 1. Seven kilometers north of Zacualtipan, Hidalgo. = *T. phenax halophilus*.
- hammondi*, *Eutaenia*. Kennicott, *Proc. Acad. Nat. Sci. Phila.*, 1860, p. 322. San Diego and Ft. Tejon, California. = *T. hammondi*.
- Haydenii*, *Eutaenia*. Kennicott, *Expl. Surv. W. 100th Mer.*, vol. 12, pt. 2, 1860, p. 298. Ft. Pierre, Nebraska. = *T. radix*.
- Henshawi*, *Eutaenia*. Yarrow, *Proc. U. S. Nat. Mus.*, vol. 6, 1883, p. 152. Ft. Walla Walla, Washington. = *T. ordinoides vagrans*.
- hueyi*, *Thamnophis ordinoides*. Van Denburgh and Slevin, *Proc. Calif. Acad. Sci.*, ser. 4, vol. 13, 1923, p. 2. Arroyo Encantado, San Pedro Mártir Mts., Baja California.
- hydrophila*, *Thamnophis ordinoides*. Fitch, *Amer. Midl. Nat.*, vol. 17, 1936, p. 648. Trail Creek, Jackson Co., Oregon.
- ibibe*, *Coluber*. Daudin, *Hist. Nat. Rept.*, vol. 7, 1803, pp. 181-3. Carolina. = *T. sirtalis sirtalis*.
- infernalis*, *Coluber*. Blainville, *Nouv. Ann. Mus. Hist. Nat. Paris*, vol. 4, 1835, p. 291, pl. 23, figs. 3-3a. California. = *T. sirtalis infernalis*.
- insigniarum*, *Eutaenia*. Cope, *Proc. Amer. Philos. Soc.*, vol. 22, 1885, p. 172. Chapultepec, Distrito Federal, Mexico. = *T. macrostemma macrostemma*.
- jauresi*, *Tropidonotus*. Duméril & Bibron, *Erp. Gén.*, vol. 7, p. 606. No locality. = *T. sirtalis sirtalis*.
- Kennicotti*, *Tropidonotus*. Jan, *Elenco Sist. Ofidi*, 1863, p. 70. North America. = *T. sirtalis parietalis* (?).
- leptocephala*, *Eutaenia*. Baird & Girard, Cat. N. Amer. Rept., 1853, pp. 29-30. Puget Sound. = *T. ordinoides ordinoides*.
- lineolata*, *Eutaenia elegans*. Cope, *Proc. U. S. Nat. Mus.*, vol. 14, 1892, p. 655. Southern California. = *T. ordinoides vagrans*.
- macrostemma*, *Eutaenia*. Kennicott, *Proc. Acad. Nat. Sci. Phila.*, 1860, p. 331. Mexico City, D. F. = *T. macrostemma macrostemma*.
- marciana*, *Eutaenia*. Baird & Girard, Cat. N. Amer. Rept., 1853, pp. 36-37. Red River, Arkansas [Oklahoma]. = *T. marcianus*.
- megalops*, *Eutaenia*. Kennicott, *Proc. Acad. Nat. Sci. Phila.*, 1860, p. 330. Tucson, Arizona; Santa Magdalena, Sonora. = *T. macrostemma megalops*.
- melanogaster*, *Tropidonotus*. Peters, *Monatsb. Berl. Akad. Wiss.*, 1864, pp. 389-390. Mexico. = *T. melanogaster melanogaster*.
- melanota*, *Eutaenia sirtalis*. Higley, *Trans. Wisc. Acad. Sci. Arts Lett.*, vol. 7, 1889, p. 163. Walworth Co., Wisconsin. = *T. sirtalis sirtalis*.
- melanotaenia*, *Eutaenia radix*. Cope, *Proc. U. S. Nat. Mus.*, vol. 11, 1889, pp. 400-401. Brookville, Indiana. = *T. radix*.
- mesomelanus*, *Tropidonotus*. Jan, *Elenco Sist. Ofidi*, 1863, p. 73. Mexico. = *T. melanogaster melanogaster*.
- multimaculatus*, *Atomarchus*. Cope, *Amer. Nat.*, vol. 17, 1883, p. 1300. San Francisco River, New Mexico, near Arizona Boundary. = *T. rufipunctatus*.
- nigrolateris*, *Eutaenia*. Brown, *Proc. Acad. Nat. Sci. Phila.*, 1889, pp. 421-2. Tucson, Arizona. = *T. marciana*.
- nigrilatus*, *Eutaenia*. Cope, *Proc. U. S. Nat. Mus.*, vol. 14, 1892, p. 665. Tucson, Arizona. = *T. marciana* (emendation of *nigrolateris* Brown).
- obalskii*, *Tropidonotus*. Mocquard, *Bull. Mus. Hist. Nat. Paris*, 1903, no. 5, pp. 211-2. Black Lake, Canada. = *Thamnophis sirtalis sirtalis*.
- obscura*, *Eutaenia sirtalis*. Cope, *Expl. Surv. W. 100th Mer.*, vol. 5, p. 546. Westport, New York; Lacque Parle, Minnesota; Ft. Benton, Montana; California. = *T. sirtalis sirtalis*. The name is here restricted to the five co-types (U.S.N.M. No. 974) from Westport, New York.
- ocellata*, *Eutaenia cyrtopsis*. Cope, *Bull. U. S. Nat. Mus.*, no. 17, 1880, pp. 22-23. Helotes, Bexar Co., Texas. = *T. eques cyrtopsis*.
- olympia*, *Thamnophis leptocephalus*. Meek, *Zool. Ser. Field Mus. Nat. Hist.*, vol. 1, 1899, p. 235. Olympic Mts., Washington. = *T. ordinoides ordinoides*.
- ordinatus*, *Coluber*. Linnaeus, *Syst. Nat.*, ed. 12, vol. 1, 1766, p. 379. Carolina. = *T. sirtalis sirtalis*.
- ordinoides*, *Tropidonotus*. Baird & Girard, *Proc. Acad. Nat. Sci. Phila.*, 1852, p. 176. Puget Sound. = *T. ordinoides ordinoides*.

- ornata*, *Eutaenia*. Baird, Rept. U. S. Mex. Boundary, 1859, p. 16, pl. 9. Indianola, Texas; Lower Rio Grande, Texas; San Antonio, Texas. = *T. sirtalis parietalis*.
- pallidula*, *Thamnophis sirtalis*. Allen, *Proc. Bost. Soc. Nat. Hist.*, vol. 29, 1899, pp. 64-67. Intervale, New Hampshire. = *T. sirtalis sirtalis*.
- parietalis*, *Coluber*. Say in Long's Exp. Rocky Mts., vol. 1, 1823, p. 186. Stone Quarry on west side of Missouri River, 3 miles above the mouth of Boyer's River. = *T. sirtalis parietalis*.
- phenax*, *Eutaenia*. Cope, *Proc. Acad. Nat. Sci. Phila.*, 1868, p. 134. Córdoba, Veracruz (in error?). = *T. phenax phenax*.
- Pickeringii*, *Eutaenia*. Baird & Girard, Cat. N. Amer. Rept., 1853, pp. 27-28. Puget Sound. = *T. sirtalis pickeringii*.
- plutonia*, *Eutaenia vagrans*. Yarrow, *Proc. U. S. Nat. Mus.*, vol. 6, 1883, p. 152. Arizona. = *T. ordinoides vagrans*.
- postremus*, *Thamnophis eques*. See below. Hda. El Sabino, Michoacán.
- praeocularis*, *Eutaenia*. Bocourt, *Le Naturaliste*, 1892, p. 278. Belize, British Honduras. = *T. sumichrasti praeocularis*.
- proximus*, *Coluber*. Say in Long's Exp. Rocky Mts., 1823, p. 187. Stone Quarry on west side of Missouri River, 3 miles above the mouth of Boyer's River. = *T. sauritus proximus*.
- pulchrilatus*, *Eutaenia*. Cope, *Proc. Amer. Philos. Soc.*, vol. 23, 1885, p. 174. Probably Guanajuato. = *T. eques eques*.
- radix*, *Eutaenia*. Baird & Girard, Cat. N. Amer. Rept., 1853, p. 34. Racine, Wisconsin. = *T. radix*.
- rozellae*, *Thamnophis*. Smith, *Proc. Biol. Soc. Wash.*, vol. 53, 1940, pp. 56-57. Palenque, Chiapas. = *T. sumichrasti sumichrasti*.
- rubristriata*, *Thamnophis*. Meek, *Zool. Ser. Field Mus. Nat. Hist.*, vol. 1, 1899, p. 235. Olympic Mts., Washington. = *T. ordinoides ordinoides*.
- rufipunctatum*, *Chilopoma*. Cope, Rept. U. S. Expl. Surv. W. 100th Mer., vol. 5, 1875, p. 544. Southern Arizona. = *T. rufipunctatus*.
- rutuloris*, *Eutaenia*. Cope, *Proc. Amer. Philos. Soc.*, vol. 22, 1885, pp. 388-9. Cozumel Island. = *T. sauritus chalcus*.
- saurinii*, *Eutaenia*. Kennicott, *Proc. Acad. Nat. Sci. Phila.*, 1859, p. 98. Florida. = *T. sauritus sackenii*.
- saurita*, *Coluber*. Linnaeus, *Syst. Nat.*, ed. 12, vol. 1, 1766, p. 385. Carolina. = *T. sauritus sauritus*.
- scalaris*, *Thamnophis*. Cope, *Proc. Acad. Nat. Sci. Phila.*, 1860, p. 369. Jalapa, Veracruz. = *T. scalaris scalaris*.
- scaliger*, *Tropidonotus*. Jan, Elenco Sist. Ofidi, 1863, p. 70. No type locality. = *T. scalaris scaliger*.
- semifasciata*, *Eutaenia sirtalis*. Cope, *Proc. U. S. Nat. Mus.*, vol. 14, 1892, pp. 662-3. Aux Plaines, Illinois. = *T. sirtalis sirtalis*.
- sirtalis*, *Coluber*. Linnaeus, *Syst. Nat.*, ed. 10, vol. 1, 1758, p. 222. Canada. = *T. sirtalis sirtalis*.
- stejnegeri*, *Thamnophis*. McLain, *Contr. Neotr. Herp.*, 1899, pp. 4-5, pl. Salamanca, Guanajuato. = *T. macrostemma megalops*.
- sumichrasti*, *Eutaenia*. Cope, *Proc. Acad. Nat. Sci. Phila.*, 1866, p. 306. Orizaba, Veracruz (in error?). = *T. sumichrasti sumichrasti*.
- taenia*, *Coluber*. Schoepf, *Reise Ver. Staat.*, 1788, vol. 1, p. 496. New York (?). = *T. sirtalis sirtalis*.
- tetrataenia*, *Eutaenia sirtalis*. Cope, U. S. Expl. Surv. W. 100th Mer., vol. 5, 1875, p. 546. Puget Sound, Washington; Pitt River, California. = *T. sirtalis tetrataenia*.
- trilineata*, *Eutaenia sirtalis*. Cope, *Proc. U. S. Nat. Mus.*, vol. 14, 1892, p. 665. Port Townsend, Oregon. = *T. sirtalis concinnus*.
- trivittatus*, *Tropidonotus*. Hallowell, *Proc. Acad. Nat. Sci. Phila.*, 1853, p. 237. Cosumnes River, California. = *T. ordinoides elegans*.
- twiningi*, *Eutaenia radix*. Coues and Yarrow, *Bull. U. S. Geol. Surv.*, vol. 4, pp. 279-280. Two Forks of Milk River, Montana. = *T. radix*.
- vagrans*, *Eutaenia*. Baird & Girard, Cat. N. Amer. Rept., 1853, p. 35. California, in error. = *T. ordinoides vagrans*.
- vicinus*, *Thamnophis*. See below. Temaxcal, Michoacán.
- vidua*, *Eutaenia infernalis*. Cope, *Proc. U. S. Nat. Mus.*, vol. 14, 1892, p. 658. San Francisco, California. = *T. ordinoides atratus*.

Jan's *Tropidonotus intermedius* (Elenco Sist. Ofidi, 1863, p. 70, and *Arch. Zool. Anat. Fis.*, vol. 3, 1865, p. 209), from unknown locality, was placed, with question, in the synonymy of *marcianus* by Boulenger (Cat. Snakes, vol. 1, 1893, p. 210). This disposition cannot be correct. The snake is described as follows (translation). "This serpent, of unknown provenance, differs principally from *T. natrix*, which it resembles not a little, by having 8 supralabials and 21 series of scales. Behind the head are seen two spots that simulate a kind of collar, and on the body six series of small spots disposed alternately. Both upper and lower labials have a black border on lip; the predominant tint is olive-color above and yellowish below. The specimen examined is 74 centimeters long, of which 14 centimeters and 5 millimeters form the tail." It is inferred from this description that the anal is divided as in *T. natrix*, with which *intermedius* is identical except in the characters mentioned; it is likewise apparent that no light stripes exist in the described specimen (lacking in *natrix*). I believe the name is based upon some species which does not occur in the western hemisphere.

### *Thamnophis phenax phenax* Cope.

The five specimens known of this form are from "Córdoba" (Nos. 30498-9) and "Alpine Region, Orizaba" (No. 7079[3]). I believe the former locality is incorrect, as it is situated at an elevation of some 2,000 ft., in a humid forest zone.

The subspecies is different from all other *Thamnophis* in having the large dorsal

blotches completely crossing the back. One specimen is of great interest, as in it the pattern is partially broken, and shows a stage intermediate between the striped pattern of most species and the singular one of *phenax*. Only the nuchal blotch is single; on the anterior half of the body the blotches are divided medially and alternate with each other, and a very irregular, zig-zag median stripe is made evident; at the middle of the body a median series of blotches, similar to the lateral blotches, becomes evident; and on the extreme posterior part of the body this median series of spots is divided into two, forming a total of four series of alternating spots on the body. An additional series of poorly defined spots occurs on each side, involving the outer two or three rows of scales, but these are visible also in the other specimens of *phenax*. The pattern of this aberrant specimen is highly suggestive of a primitive status for the typical *phenax* pattern, from which the striped patterns, with six series of spots, observable in all other *Thamnophis*, may have been derived.

#### Scale Counts of *phenax phenax*.

Number	Sex	Scale Rows	Ventrals	Caudals	Supralabials	Infralabials	Proc.	Ptoc.
30499	♀	19-19-17	161	65	8-8	9-9	1-1	3-3
7079	♀	19-19-17	151	60	8-8	11-11	1-1	3-3
7079	♂	17-19-17-15	160	78	7-7	10-10	1-1	3-3
7079	♂	19-19-17	158	76	8-8	9-10	1-1	3-4
30498	♂	19-19-17	158	73	7-7	9-10	1-1	3-3

#### *Thamnophis phenax halophilus* Taylor.

In addition to the type, one other specimen is known, from Tequeyutepec, 7 miles west of Jalapa, Veracruz, at 5,600 ft. (No. 110801). It is a male, with 19-19-17 scale rows, 156 ventrals, 71 caudals, 8-8 supralabials, 11-12 infralabials, one preocular, three postoculars. The head has the pattern of *phenax*, with small, parietal spots and most of the remainder of the head light. A pair of large nuchal spots is present, and following these on each side is a double series of very small spots which decrease in size and distinctness posteriorly.

In structural characters and form of body the present form is not distinguishable from *phenax*. It also has the same, peculiar head pattern. The differences between the two are in body pattern; *halophilus* shows but little evidence of spots, while in *phenax* they usually are present, as a single series. A specimen of *phenax* shows a condition intermediate between the two pattern types, however, and accordingly I have little doubt that *halophilus* is properly associated as a subspecies of *phenax*. The trend exhibited by *halophilus*—toward reduction of pattern by subdivision and obsolescence of the spots—is exhibited also by a subspecies of *scalaris* (*godmani*).

Most distinctive of *halophilus* and *phenax* is the peculiar head pattern, by which they easily are distinguished from close relatives.

#### *Thamnophis scalaris* Cope.

The most diminutive garter snake in Mexico is *Thamnophis scalaris*, a species distinguished not only by its small size but also by its reduced number of supralabials (normally seven, rarely eight), very small, low loreal, a relatively small eye and head, and the tendency toward formation of a single row of large spots on each side to replace the usual double row. A median stripe is always present, but the lateral stripe is poorly defined or invisible, on the second and third scale rows (or second only) when visible. These characters define a form restricted to high elevations (conifer zone) on the central Mexican plateau.<sup>1</sup>

Since the areas to which these snakes are adapted are separated from each other by broad barriers in the form of semi-arid deserts and plains, a gradual divergence in different directions from the presumably

more uniform character of the original stock has taken place in the various isolated populations. As a result three very well defined populations may be distinguished.

#### *Thamnophis scalaris scalaris* Cope.

**Diagnosis.** Supralabials usually seven; eye relatively small; scale rows usually 17-19-15; ventrals 134 to 145 in males, 136 to 145 in females; caudals 69 to 77 in males, 53 to 65 in females; usually a single row of spots on each side at least anteriorly; two vertical light lines, one on nape and one behind eye, enclosing a lateral extension of dorsal head color reaching to upper edge of labials; dorsal stripe splitting the two nape spots, or else a complete transverse light band preceding the fused nape spots.

**Specimens Examined.** Thirty, as follows: Orizaba (Nos. 7076, 12115-6, 30497), Cruz Blanca (No. 110806, EHT-HMS No. 4989), Mt. Orizaba (FMNH Nos. 1517, 1523), Las Vigas (EHT-HMS No. 27916), Cofre de Perote (EHT-HMS No. 5567), Veracruz; Mt. Orizaba, western side, 10,000 ft. (EHT-

<sup>1</sup> The specimens mentioned by Ruthven (*op. cit.*, p. 129) from Guatemala are not *scalaris* but belong to a subspecies of *sumichrasti* (*fulvus*). They are discussed under the latter name in the following.

HMS No. 5566), *Puebla*; El Chico National Park (EHT-HMS No. 23512), Guerrero (EHT-HMS No. 5568), *Hidalgo*; Mt. Popocatepetl (No. 110815), Lake Zempoala (No. 110816, EHT-HMS Nos. 5299, 5565, 21535), *Mexico*; Tres Cumbres (EHT-HMS No. 4964), Km. 54, 26 kilometers east of Cuernavaca (EHT-HMS No. 4666), *Morelos*. No locality, EHT-HMS No. 23513. Data available also on ANSP No. 11694, Jalapa, Veracruz (Ruthven, *op. cit.*, p. 129), and the type (Cope, *loc. cit.*)

*Variation.* Usually the spots are in a single series on each side at least anteriorly, but some variation occurs. In certain specimens two rows are visible the entire length of the body (save the nuchal spots), and in some of these the posterior spots become very indistinct. The essential features of the head pattern are the two vertical light bars (one postocular and one on nape) which enclose an extension of the dorsal head color reaching the upper edges of the supralabials; the nape spots are completely separated by the continuation of the middorsal light stripe to the occiput, or else the two nuchal light bars are prolonged and are fused medially in front of the fused nuchal spots.

In some respects the type, as described by Cope, is not exactly typical of the subspecies; among other discrepancies are the 8-8 supralabials. There is, however, no other

known species of *Thamnophis* in that area to which the name may apply. One other specimen with 8-8 supralabials has been seen.

*Thamnophis scalaris godmani*  
(Günther).

*Diagnosis.* Supralabials usually seven; eye relatively small; scale rows usually not over 17, usually 15 or less in front of anus; ventrals 134 to 158; caudals 61 to 88 in males, 60 to 73 in females; head dark above, the color extending posteriorly to a transverse black line across nape, and posterolaterally to level of angle of mouth.

*Specimens Examined.* Twenty-six from the states of *Puebla* (San Diego, No. 110810; Laguna San Bernardino (EHT-HMS Nos. 27932-4); Pájaro Verde (No. 110811, EHT-HMS No. 23801); *Oaxaca* (Oaxaca, Nos. 46534, 46604, EHT-HMS Nos. 23774-5; Cerro San Luis, EHT-HMS No. 4997, Cerro San Felipe Summit, EHT-HMS Nos. 15978, 15989); *Veracruz* (above Acultzingo, Nos. 110807-9, EHT-HMS Nos. 5277-9, 5280-1, 27932-4) and *Guerrero* (Omiteme, EHT-HMS Nos. 23779, 23781). Ten other specimens (including the types) are recorded by Boulenger (Cat. Snakes Brit. Mus., vol. 3, 1896, p. 600) from Omiteme, Guerrero, and certain data given.

*Description* (from No. 46534). Head

Scale Counts in *scalaris scalaris*.

Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.
1517	♂	17-17-15	138	74	7-7	9-9	1-1	2-2
1517	♂	17-17-15	137	75	7-7	8-8	1-1	3-3
1517	♂	17-17-15	138	75	7-7	8-9	1-1	2-2
7076	♂	17-17-15	142	73	7-7	9-9	1-1	2-3
7076	♂	17-19-15	137	72	7-7	9-9	1-1	3-3
7076	♂	17-19-15	134	76	7-7	8-9	1-1	3-3
11694	♂ ?	17-19-15	138	73	7-7	9-9	1-1	3-3
30497	♂	17-19-15	145	75	7-7	10-10	1-1	3-3
110806	♂	17-19-15	136	77	7-8	9-10	1-1	3-3
4989	♂	17-19-17	138	—	7-8	9-10	1-1	3-3
5568	♂	17-19-17	137	74	7-7	8-8	1-1	3-3
23513	♂	17-19-17	140	73	7-7	9-9	1-1	3-3
5565	♂	19-19-17	133	69	7-7	9-10	1-1	2-3
21535	♂	17-19-15	142	74	7-7	9-9	1-1	3-3
5299	♂	17-19-16	137	70	7-8	10-10	1-1	2-3
23512	♀	17-19-16	145	63	7-7	9-10	1-1	3-3
5567	♀	17-19-15	139	60	7-7	9-9	1-1	3-3
5566	♀	19-19-16	140	58	7-7	9-9	1-1	3-3
110815	♀	17-19-17	144	61	7-7	10-10	1-1	3-3
110816	♀	17-19-17	136	58	7-7	10-10	1-1	3-3
4666	♀	17-19-16	141	—	7-7	8-9	1-1	2-3
4964	♀	17-19-17	140	54	7-7	10-10	1-1	3-3
1517	♀	17-19-16	141	61	7-7	9-10	1-1	3-3
1517	♀	17-19-15	136	65	7-7	9-10	1-1	3-3
1517	♀	17-19-15	140	66	7-7	9-9	1-1	3-3
1517	♀	17-19-15	138	60	7-7	8-8	1-1	2-3
1523	♀	17-19-17	144	61	7-7	9-9	1-1	2-3
7076	♀	17-19-15	145	58	7-8	10-10	1-1	3-3
12115	♀	17-19-15	135	59	7-7	9-9	1-1	3-3
12116	♀	17-19-17	136	53	7-7	9-9	1-1	2-3
Type	♀ ?	?-19-?	143	59	8-8	10-10	1-1	3-3

small, not markedly distinct from neck, short; suture between internasals equal to that between prefrontals; internasals about three-fourths as long as prefrontals, a little over half their area; latter extending far onto sides of head; preocular not in contact with frontal; latter hexagonal, shorter than its distance from tip of snout, more than twice as long as broad; nasal completely divided; loreal small (fused with prefrontal on one side); a single large preocular; three postoculars; temporals 1-2; supralabials 7-7, third and fourth entering eye; eye small, its vertical diameter a third greater than its distance from labial border, less than height of fifth labial; longitudinal diameter of eye (3.1 mm.) over half its distance from tip of snout (5.7 mm.); infralabials 9-10, 4-5 in contact with anterior chinshields; latter shorter and a little broader than posterior chinshields, which are separated medially.

Dorsals in 17-17-16 rows, all of which are keeled; ventrals 147; caudals 64; total length 459 mm., tail 106 mm.

Top of head uniform brown, the color extending onto nape a distance of four scale lengths, where it is bordered by a black, transverse line; lips nearly white, except for black lines along the sutures between the labials; a very distinct, broad black line bordering penultimate labial above and posteriorly; dorsal color extending posterolaterally even with angle of mouth, uninterrupted save by a vague lighter area immediately posterior to penultimate labial; be-

ginning after transverse nape line, a light (brown) vertebral line on middorsal scale row, visible to tail; sides of body brown, of about same shade as top of head, becoming lighter on first and second scale rows, the color disappearing on ends of ventrals; two rows of very small, scarcely distinguishable, alternating spots on each side; the spots of lower row involving the third and fourth scale rows, the upper ones the seventh and eighth scale rows; the spots are more distinct anteriorly than posteriorly. Belly and subcaudal surface dark slate; chin and throat cream; no black ventral marks save on the extreme anterior edges of ventrals (visible only by lifting overlapping portion of preceding ventrals).

*Variation.* The 25 other specimens examined show scarcely any divergence from the pattern of the described specimen. One, softer than the others, shows the lateral dark spots more plainly. In three the nuchal spots characteristic of *scalaris* and many other *Thamnophis* are visible, being darker than the dorsal head color; in No. 46534 they are fused indistinguishably with the head color. The vertical dark bars are not regularly present on the anterior labials, but a curved line on the edge of the sixth labial is regularly present and the most distinct of all.

The specimen with 19 scale rows has a short series of abnormally small scales intercalated on either side of the vertebral

#### Scale Counts in *scalaris godmani*.

Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.
5279	♂	17-17-15	153	76	7-7	10-10	1-1	2-3
46534	♂	17-17-16	147	64	7-7	9-10	1-1	3-3
46604	♂	17-19-17-15	147	—	7-7	10-10	1-1	3-3
110807	♂	17-17-15	145	65	7-7	10-10	1-1	3-3
110808	♂	17-17-15	149	75	7-7	10-10	1-1	3-3
Brit. M.	♂		148	80	7-7			
Brit. M.	♂		146	74	7-7			
Brit. M.	♂		146	81	7-7			
Brit. M.	♂		146	78	7-7			
Brit. M.	♂		149	73	7-7			
Brit. M.	♂		145	81	7-7			
5277	♂	17-17-15	152	76	7-7	10-10	1-1	3-3
5280	♂	17-17-14	158	77	7-7	10-10	1-1	3-3
5281	♂	17-17-15	150	73	7-7	10-11	1-1	3-3
23775	♂	17-17-15	143	65	7-7	10-10	1-1	3-3
23779	♂	17-17-15	142	88	7-7	10-10	1-1	3-4
23774	♂	17-17-15	149	61	7-7	9-9	1-1	3-3
15989	♂	17-17-15	146	65	7-7	10-10	1-1	3-3
5278	♀	17-17-15	151	68	7-8	10-10	1-1	3-3
23781	♀	17-17-15	136	71	7-8	10-10	1-1	3-3
15978	♀	17-18-16	143	63	6-7	10-10	1-1	3-3
23801	♀	17-17-15	143	64	7-7	9-10	1-1	3-3
110809	♀	17-17-11	141	64	8-8	9-10	1-1	2-3
11022	♀	17-17-14	140	57+	7-7	10-10	1-1	3-3
11551	♀	17-17-15	144	60	7-7	9-10	1-1	3-3
Brit. M.	♀		142	66	7-7			
Brit. M.	♀		145	73	7-7			
Brit. M.	♀		134	61	7-7			
Brit. M.	♀		141	—	7-7			
4997	♀	17-17-15	141	—	7-7	9-10	1-1	3-3

row. One specimen has the penultimate and antepenultimate labials mostly fused. The one with 8-8 supralabials owes its higher count to the presence of a small (but complete) labial between the second and third labials.

*Comparisons.* In scale characters this form is most like *s. scalaris*, but it differs from that by usually having no more than 17 scale rows; typical *scalaris* usually has 19 near the middle of the body. In details of head pattern the two are remarkably and constantly different. Typical *scalaris* has the median light stripe usually extending to the occiput, separating the nuchal blotches; if it does not reach the occiput the light areas bordering the nape spots anteriorly meet dorsally. Also a light, vertical, postocular band extends dorsally, to the supraocular; the dorsal head color extends laterally between this postocular and the nuchal light lines, and terminates abruptly at the upper edge of the supralabials.

### *Thamnophis scalaris scalariger* (Jan).

*Diagnosis.* Supralabials usually seven; eye relatively small; scale rows usually 19-19-17, never 17-17-15, occasionally 17-19-17, rarely 17-19-15; ventrals 136 to 151 in males, 135 to 150 in females; caudals 51 to 74 in males, 47 to 65 in females; a single row of spots on each side, seldom two rows; spots as a rule larger, more rectangular, than in *s. scalaris*; head pattern as in latter.

*Specimens Examined.* Seventeen, from Mexico City (No. 12730) and Road between Tacubaya and Desierto de los Leones (EHT-HMS No. 5298), *Distrito Federal*; 15 kilometers west of Toluca (Nos. 110812-4), Toluca (No. 32281), Río Frio (EHT-HMS Nos. 4990, 21524), Llano Grande near Río Frio (EHT-HMS Nos. 23510-11), and 8-10 miles west of Villa Victoria (EHT-HMS

No. 5571), *México*; Mt. Malinche (EHT-HMS Nos. 5569-5570), *Tlaxcala*; Guanaajuato No. 12675); 2 miles east of Río Frio, *México*, in *Puebla* (Nos. 110817-8); and Nahuatzen (No. 46553), *Michoacán*.

*Variation.* In cephalic pattern this subspecies is like *s. scalaris*. In general its body pattern also is the same, except that the lateral spots are more frequently large and single.

*Comparisons.* This form differs from *s. scalaris* primarily in the number of scale rows anteriorly and in front of anus; males may usually have more numerous caudals and ventrals. The race is conceived to have a central area of distribution, away from the periphery of the plateau; *s. scalaris* occupies the eastern escarpment, which for the most part is separated by arid plains from the central area where *s. scalariger* occurs; *s. scalaris* also occurs on the southern edge of the plateau in Morelos and *México*. Further specimens from central *Michoacán* will be necessary to determine whether the Nahuatzen, *Michoacán*, specimen is properly allocated with *s. scalariger*.

The name *scalariger* is applied to the central subspecies of *scalaris* with some question. The scale rows are said to be 19 in the type, which therefore is not the same as *godmani*. However, it is impossible to certainly ascertain which of the other two subspecies the type may represent. The only indication whatever is the statement that the spots are large and "subquadrate." While this statement is applicable to some specimens of typical *scalaris*, on the other hand in general it more clearly describes the central subspecies. Boulenger's description of *scalariger* (Cat. Snakes, vol. 1, 1893, pp. 203-204) is of no assistance, but is apparently a composite based perhaps upon *scalariger* and *godmani* as well.

### Scale Counts in *scalaris scalariger*.

Number	Sex	Scale Rows	Ventrals	Caudals	Supralabials	Infralabials	Proc.	Ptoc.
12675	♂	19-17-15	144	56	7-7	9-9	1-1	2-2
12730	♂	19-17-17	151	52	7-7	9-9	1-1	2-3
32281	♂	19-19-17	143	52	7-7	9-9	1-1	3-3
110814	♂	17-19-17	143	51	7-7	9-10	1-1	2-3
5570	♂	19-19-17	140	74	7-7	10-10	1-1	3-3
5571	♂	19-19-17	136	71	7-7	10-10	1-1	2-3
46553	♀	17-19-17	139	57+	7-7	10-10	1-1	3-3
110812	♀	19-19-17	135	47	7-7	9-9	1-1	2-3
110813	♀	19-19-17	138	—	6-7	8-8	1-1	2-2
110817	♀	19-19-17	143	57	7-7	10-10	1-1	3-3
110818	♀	19-19-17	149	62	7-7	8-9	1-1	3-3
5569	♀	19-19-17	146	55	8-8	9-12	1-1	3-3
23510	♀	19-19-17	142	—	7-7	9-9	1-1	3-3
4990	♀	19-19-17	143	58	7-7	10-10	1-1	3-3
23511	♀	19-19-17	150	64	7-7	10-10	1-1	3-3
21524	♀	19-19-17	144	65	8-8	10-10	1-1	3-3
5298	♀	18-19-17	137	49+?	7-7	9-10	1-1	2-2



The three subspecies of *scalaris* may be contrasted as follows:

	<i>scaliger</i>	<i>scalaris</i>	<i>godmani</i>
Posterior scale rows, less than 17	6% (1 in 17)	70% (21 in 30)	100% (18)
Maximum scale rows 19	100% (17)	87% (27 in 31)	6% (1 in 18)
Anterior scale rows 17 <sup>2</sup>	12% (2 in 17)	93% (28 in 30)	100% (18)
Caudals in males over 60	33% (2 in 6)	100% (14)	100% (16)
Ventrals in males 143 or more	67% (4 in 6)	7% (1 in 15)	94% (16 in 17)
Infralabials 10 or more on each side	42% (7 in 17)	23% (7 in 31)	72% (13 in 18)

<sup>2</sup> Some care must be used in determining this character, for the distance on neck in which the scale rows are reduced to 17, in *s. scalaris* and *s. scaliger*, is very short.

This tabulation does not include pattern characters, by which *godmani* can easily be distinguished from the other two. Curiously, no differences of great significance are discernible in the ventral and caudal counts of the females of the three subspecies.

### *Thamnophis chrysocephalus* (Cope).

This is one of the few species of the genus entirely lacking a vertebral light stripe, and the only one that combines this character with 17–15 scale rows. Also characteristic of the species is the very light color of the head, sharply differentiated from the black nuchal area. The lateral stripe has irregular edges and involves the second and third scale rows.

Ordinarily the dorsum, between the lateral stripes, is light brown or brownish-gray, with two series of very poorly defined spots on each side; the spots in the outer series are generally better defined than those of the inner series; posteriorly the spots become entirely indistinguishable; anterior edges of ventrals irregularly marked with black. However, another color phase is represented by the type of *eburatus*, in which the whole dorsum (between the stripes) is dark (black), and the entire venter black. This phase appears to be only a variation, since (1) it occurs in a series of specimens from other localities, one in seven from "Orizaba," and one in three from the vicinity of Acultzingo, Veracruz; and (2) it does not regularly occur in the region of the type locality. Moreover the specimens having the very dark color are otherwise precisely like other specimens with the lighter markings; the differences are only in degree of pigmentation, and do not involve different patterns.

Twenty-three specimens examined are from the following localities. *Veracruz*: Orizaba (Nos. 7077, 30494); above Acultzingo (EHT-HMS Nos. 21536–8; U.S.N.M. No. 110774); Xuchil (F.M.N.H. No. 1519). *Oaxaca*: Cerro San Felipe (EHT-HMS No. 5556); Totontepec (No. 46445); Mt. Zempoaltepec (No. 46446). *Puebla*: Pájaro Verde (Nos. 110775–6). *Guerrero*: Omilteme (Nos. 46342, 47747; EHT-HMS Nos. 23778, 23780, 23782).

### *Thamnophis vicinus* sp. nov.

*Holotype*. EHT-HMS No. 21539, female, from a locality near Temaxcal, Michoacán, about 20 kilometers east of Morelia, collected by E. H. Taylor, August, 1939. *Paratypes*. Nine, including No. 15897, a topotype, and Nos. 15893–6, 15992–5, from Morelia, Michoacán, all collected by H. Devlin Thomas.

*Diagnosis*. Similar to *e. eques*, having 19–19–17 scale rows, 149 to 160 ventrals and 77 to 89 caudals; differing from *e. eques* in the complete absence of a middorsal light stripe which is replaced by a series of dark spots, and perhaps in having a smaller size.

*Description of Holotype*. Head a half wider than neck, somewhat flattened; eye large, its longitudinal diameter (3.2 mm.) three-fourths its distance from tip of snout (4 mm.); full width of rostral visible from above; length of portion of rostral visible from above about half length of internasals; latter about half as wide anteriorly as posteriorly, a little shorter than maximum length of prefrontals; frontal somewhat shield-shaped, a little longer (4.2 mm.) than its distance from tip of snout (3.8 mm.), subequal to length of median suture between parietals, four-fifths maximum length of parietals (5.3 mm.), its width about two-thirds (2.7 mm.) its length; supralabials 7–8, three on one side to a point below middle of eye, four on other; antepenultimate labial slightly the largest; nasal completely divided, naris in anterior section, which is a little higher and a little larger than posterior section; a quadrangular loreal, a little higher than wide; a large preocular, narrowly separated from frontal; three postoculars, more or less subequal in size, the upper two in contact with parietal; temporals 1–2–3, the primary much larger than others. Infralabials 10–10, five in contact with anterior chinshields, two (5th and 6th) with posterior; latter separated from each other medially throughout their length, and divergent posteriorly; posterior chinshields perhaps somewhat longer than anterior, latter a little the wider.

Dorsal scales strongly keeled, except those in outer row, which are weakly keeled; dorsals in 19–19–17 rows, those scales toward middorsum with a single apical notch, none with pits; ventrals 151; anal entire; caudals 77; total length 299 mm., tail 76 mm.



Top of head light slate, this color merging with cream on sides of head and white on lower parts of labials; posterior edges of supralabials with a vertical black line, that on antepenultimate labial most conspicuous; a large, single, black nuchal spot extending laterally two scales below angle of mouth, anteriorly to within one scale length of rictus oris and to posterior margin of parietals, and posteriorly five scale lengths (medially); middorsum of body brown, this color reaching to the third scale row, where it is replaced by a very light brown or cream color; the first scale row and the lower half of the second is gray; on the posterior part of the body the lateral light stripe descends to the first and second scale rows; nowhere is the lateral light stripe sharply defined, and on the anterior third of body it is broken by encroaching black spots and with difficulty can be discerned as a stripe; three series of more or less rounded black spots, none with sharply defined edges, on the body; spots in the median series alternating with those of the lateral series; on the first scale row and lateral edges of ventrals another series of smaller black spots alternating with the lateral spots; latter spots extending to first scale row on anterior fourth of body, but posterior to this part become restricted to the area above the lateral light line; all spots becoming very poorly defined near middle of body, and posteriorly scarcely distinguishable; on the posterior part of the body the dorsum appears almost uniform brown; dorsal surface of tail brown, unspotted.

Ventral surface of head cream; belly and subcaudal surfaces slate, clouded, without distinct black markings.

*Variation.* The paratypes are very much like the holotype in coloration and scutellation. All completely lack evidence of a middorsal stripe, and the lateral stripes are poorly defined because of encroachment upon them by the lateral dark spots. The middorsal area is occupied by a series of large dark spots. The largest specimen (a male) measures 592 mm. in total length, the tail 155 mm.

*Remarks.* This species bears a very close resemblance, in coloration, to *chrysocephalus*, with which the specimens at first were associated, without question, until counts were made. These reveal a relationship closer to *eques* than to *chrysocephalus*, since the latter regularly has 17-17-15 scale rows. An examination of the maxilla also shows a closer agreement with *eques*, since the latter (4 specimens) has 24 to 27 teeth, *chrysocephalus* (2 specimens) 29 to 30, and the type of *vicinus* 26. Its chief difference from *e. eques* is the total absence of the middorsal light stripe (a middorsal series of dark spots instead); correlated with this is the reduction of the lateral light stripes.

The total absence of variation in the numerous specimens examined of *eques* with respect to the character of the middorsal stripe leads me to believe that the specimens referred to *vicinus*, even though known from a very small area, are not merely variations from the *eques* norm but represent a distinct population. The uniformity of character of the several specimens of *vicinus* also points to the probable distinctness of that species.

Since *vicinus* is so like *e. eques* from the same area in scutellation, the two might be considered subspecies; this arrangement is not supported, however, by the existence of perfectly typical *e. eques* at exactly the same localities as those in which *vicinus* has been collected. For the present they must be considered distinct species.

It seems that *vicinus* furnishes evidence of a close relationship between *eques* and *chrysocephalus* in the west, and of the derivation of one of these from the other (or from their very close ancestors). There is a southward gradient in the reduction of the median stripe, from *eques cyrtopsis* in the north, with a broad stripe, to typical *e. eques* with a narrow stripe, *vicinus* without a stripe, and *chrysocephalus* on the extreme south, also without a stripe. A similar gradient in reduction of the number of ventrals also is evident. That *vicinus* forms a connecting link in this chain is evident, but evidence that *chrysocephalus* and *eques* actually intergrade is completely lacking, and it is

#### Variation in Scale Counts of *vicinus*.

Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.	Temp.
21539	♀	19-19-17	151	77	7-8	10-10	1-1	3-3	1-2-3
15992	♀	19-19-17	149	79	8-8	10-10	1-1	3-3	1-2-3
15895	♀	19-19-17	156	80	8-8	10-10	1-1	3-3	1-2-3/4
15894	♀	19-19-17	152	78	8-8	10-10	1-1	3-3	1-2-3
15993	♂	19-19-17	162	—	8-8	10-10	1-1	3-3	1-2-3
15893	♂	19-19-17	160	84	8-8	10-10	1-1	4-4	1-2-3
15897	♂	19-19-17	161	88	8-8	9-9	1-1	3-4	1-2-3/2
15994	♂	19-19-17	155	84	8-8	10-10	1-1	4-4	1-2-3/4
15896	♂	19-19-17	160	89	8-8	10-10	1-1	3-3	1-2-3
15995	♂	19-19-17	156	86	8-8	9-9	1-1	3-3	1-2-3

assumed that such intergradation does not occur; the completely overlapping ranges bear out this assumption. However, given that orthogenetic trends do exist in this group of the genus, it is not even yet obvious in which direction evolution has occurred; conclusions by Fitch and Ruthven point toward a north-south direction in this case, while various facts mentioned elsewhere in this paper support the opposite view.

### *Thamnophis eques eques* (Reuss).

This form is characterized by having 19 scale rows; median light stripe on body very distinct and occupying no more than a single scale row; lateral light stripes on scale rows two and three; a light head followed by two large, black nape spots (fused or not); belly nearly immaculate; ventrals 146 to 171 in males, 145 to 163 in females; caudals 74 to 104 in males, 68 to 95 in females. It ranges from central Durango and southern Sinaloa southward to the edge of the plateau in Michoacán, west to Hidalgo and central Veracruz; highlands of central

Oaxaca and the Sierra Madre del Sur of central Guerrero.

*Thamnophis e. eques* can be differentiated from the northern race (*e. cyrtopsis*) by having 166 or fewer ventrals in males (97%, 31 out of 32) while in *e. cyrtopsis* only 14% (3 in 21) have 166 or fewer; in females 100% of *e. cyrtopsis* have 163 or more ventrals, while in *e. eques* 3% (1 in 38) have more than 162 ventrals.

*Thamnophis eques*, as previously known, shows a north-south trend in (1) reduction of ventral scale counts; (2) reduction of the median stripe and complete restriction of it to the vertebral scale row; and (3) reduction in an average number of supralabials. Most marked of all these trends is the reduction in ventral scale count, which shows a rather abrupt change in central Mexico. The approximate line at which this change occurs does not correspond exactly in position with the zone in which a change in the width of the dorsal stripe occurs; nevertheless, because of the ease of definition of the scale character, this is the one upon which the definition of the two races is

### Scale Counts in *e. eques* (females).

Museum	Number	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.	State
FMNH	17110	159	—	8-8	10-10	1-1	3-3	D. F.
USNM	46482	156	91	8-8	10-10	1-1	3-3	Dgo.
EHT-HMS	5282	153	89	7-8	10-10	1-1	3-3	Gto.
USNM	9892	156	91	8-8	10-10	1-1	3-4	"
"	9899	159	68	7-7	9-10	1-1	3-3	"
"	14433	151	68	7-7	10-10	1-1	3-3	"
"	14434	156	85	8-8	10-10	1-1	3-3	"
"	25363	164	73	7-7	10-11	1-1	3-3	"
"	26147	154	91	8-8	10-10	1-1	3-3	"
"	26148	155	—	8-8	10-10	1-1	3-3	"
EHT-HMS	21542	149	79	8-8	10-10	1-1	4-4	Gro.
"	23783	148	78	8-8	10-10	1-1	3-3	"
"	23792	145	79	8-8	11-12	1-1	3-4	"
"	15974	155	70	7-7	10-10	1-1	2-3	Hgo.
"	15985	158	90	8-8	10-10	1-1	3-4	"
"	23776	163	95	8-8	10-10	1-1	3-3	"
"	23785	145	85	7-8	10-10	1-1	3-3	Jal.
"	4998	156	98	8-8	11-11	1-1	2-3	"
"	5080	156	70	7-7	10-10	1-1	3-3	Mex.
"	15975	154	72	7-7	10-10	1-1	3-3	"
"	15890	152	86	8-8	10-11	1-1	3-3	Mich.
"	15891	149	87	8-8	8-10	1-1	3-3	"
USNM	110779	155	—	7-7	10-10	1-1	3-3	"
"	110780	157	71	—	—	—	—	"
EHT-HMS	21525	157	72	7-7	10-11	1-1	3-3	"
"	5276	151	83	8-8	10-10	1-1	3-3	Mor.
"	15977	150	80	8-8	10-10	1-1	3-4	"
USNM	46605	149	80	8-8	10-10	1-1	2-3	Oax.
EHT-HMS	15979	151	80	8-8	10-11	1-1	3-3	"
"	23784	158	81	7-7	10-10	1-1	3-3	"
"	23789	146	82	8-8	9-10	1-1	3-3	"
"	23790	152	77	7-8	9-10	1-1	3-3	"
"	23791	159	—	8-8	10-10	1-1	3-3	"
USNM	46457	150	—	8-8	10-10	1-1	3-3	Sin.
"	46432	160	—	7-7	10-10	1-1	3-3	Ver.
"	25038	149	75	8-8	10-10	1-1	3-3	"
"	30496	153	—	8-8	10-10	1-1	2-4	"
EHT-HMS	15986	152	—	8-8	10-10	1-1	3-4	?

largely based. The reduction in numbers of supralabials from 8 to 7 in the southern specimens is not sufficiently universal to warrant use as a key character to define a southern race. Nevertheless, specimens with 7 supralabials almost invariably belong to the southern race.

While for convenience I have here spoken of "north-south" trends, they should more properly be termed "south-north" trends for in general this is the direction of evolution in *Thamnophis* and especially in this section.

Scale counts have been taken on 104 Mexican specimens of *eques eques* and *e. cyrtopsis*. The scale rows in these are uniformly 19-19-17, except in one from "Orizaba" (with 17-19-15 rows), one from (?) Guanajuato (17-19-17 rows), one from Samachique, Chihuahua (17-19-15), two from Mojá-rachic, Chihuahua (19-19-15, 19-19-16) and one from Chilpancingo, Guerrero (19-19-16). There is no indication that these variations have special significance other than indicating the extremes of variation in the form; the extra scale rows dropped are usually missing only for a very short distance (one scale on one side, six on the other, in one case).

The identity of Reuss' name is not absolutely certain. It has generally been associated with the Mexican form here treated under that name, and at the present, until

the type can be re-examined, there is no alternative. Jan's *collaris* definitely belongs to *e. eques*, however; in it the middorsal light line is only one scale row wide (see Jan and Sordelli, Icon. Gén., livr. 25, pl. 5, fig. 2).

Specimens examined are from the following localities. *Distrito Federal*: Río San Juan de Dios (FMNH No. 17110). *Durango*: Durango (No. 8066); Huasamota (No. 46482). *Guanajuato*: Acámbaro (EHT-HMS Nos. 5282-3); Guanajuato? (Nos. 9892, 9899 [type *pulchrilatus*], 14433-4, 25363, 26147-8). *Guerrero*: 7 miles east of Chilpancingo (EHT-HMS Nos. 21542, 23783, 23786, 23792); Omilteme (EHT-HMS No. 15974); south of Zacualtipan (EHT-HMS Nos. 15985, 23776-7). *Jalisco*: 20 kilometers south of Guadalajara (EHT-HMS No. 23785); Belén (EHT-HMS Nos. 4965, 4998). *México*: Nochitongo Ditch, 30 miles north of Mexico City (No. 19003); San Martín (EHT-HMS Nos. 4968, 5080-1); Villa Victoria (EHT-HMS No. 15975); Zempoala National Park (No. 15973). *Michoacán*: 15 miles east of Morelia (EHT-HMS Nos. 15889-91, 21533-4); Los Reyes (No. 46463); Tacicuaró (Nos. 110777-83, EHT-HMS Nos. 21525-32). *Morelos*: Cuernavaca (EHT-HMS Nos. 5276, 15977). *Oaxaca*: Huajuapam (No. 46605); Summit of Cerro San Felipe (EHT-HMS No. 15979); Oaxaca (EHT-HMS Nos. 23784, 23789-91).

#### Scale Counts in *e. eques* (males).

Museum	Number	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.	State
USNM	8066	164	—	8-8	10-10	1-1	3-4	Dgo.
EHT-HMS	5283	163	101	8-8	10-10	1-1	3-3	Gto.
"	23786	157	85	7-7	10-10	1-1	4-4	Gro.
"	23788	152	81+	8-8	9-9	1-1	2-3	"
"	23777	161	95	8-8	9-10	1-1	3-4	Hgo.
"	4965	159	99	8-8	10-10	1-1	3-3	Jal.
USNM	19003	164	95	8-8	10-10	1-1	3-3	Mex.
EHT-HMS	4968	166	90	7-7	10-11	1-1	3-3	"
"	5081	159	82	7-7	9-10	1-1	3-4	"
"	15973	162	78	7-7	10-10	1-1	2-2	"
"	15889	157	97	8-8	10-10	1-1	3-3	Mich.
"	21533	171	82	7-7	9-10	1-1	3-3	"
"	21534	158	81	7-7	10-10	1-1	3-4	"
USNM	46463	155	93	8-8	10-10	1-1	3-3	"
"	110777	162	81	7-7	10-10	1-1	3-3	"
"	110778	159	80	7-7	10-10	1-1	3-3	"
"	110781	166	84	7-7	10-10	1-1	3-4	"
"	110782	146	—	7-7	9-9	1-1	2-2	"
"	110783	153	100	8-8	10-10	1-1	3-3	"
EHT-HMS	21526	159	89	8-8	10-10	1-1	3-3	"
"	21527	165	80	7-7	11-11	1-1	3-3	"
"	21528	160	79	7-7	10-10	1-1	2-2	"
"	21529	161	88	8-8	10-10	1-1	3-3	"
"	21530	159	77	7-7	10-10	1-1	3-3	"
"	21531	161	76	7-7	—	—	—	"
"	21532	163	74	7-7	10-10	1-1	3-3	"
USNM	46423	160	99	8-8	10-10	1-1	3-3	Zac.
"	32279	166	76	7-7	8-9	1-1	3-3	?
"	32280	161	78	7-7	10-10	1-1	3-3	?
EHT-HMS	5273	164	104	8-8	9-10	1-1	3-3	?
"	15976	166	—	7-7	10-10	1-1	3-3	?
"	23620	163	—	7-7	8-9	1-1	3-3	?

*Sinaloa*: Rosario (No. 46457). *Veracruz*: Las Vigas (No. 46432); Mirador (No. 25038); Totalco (EHT-HMS No. 27908); Orizaba (No. 30496). *Zacatecas*: San Juan Capistrano (No. 46423). *No locality*: (Nos. 32279-80; EHT-HMS Nos. 5273, 15976, 15986, 23620). The species has been reported also from Moro León, Guanajuato, and Tezuítlán, Puebla.

***Thamnophis eques cyrtopsis***  
(Kennicott).

This race differs from *e. eques* of the southern part of the Mexican plateau chiefly in the greater average number of ventral scales. In *e. cyrtopsis* 86% of the males have 167 or more ventrals, and 100% of the females have 163 or more ventrals; in *e. eques*, on the other hand, only 3% of the males have 167 or more ventrals, and only 3% of the females have more than 162 ventrals.

In addition, over most of its range *e. cyrtopsis* is characterized by having the middorsal light stripe involving parts of adjacent scale rows on various parts of the body; in *e. eques* the middorsal stripe is always confined strictly to the vertebral scale row. Toward the south specimens of *e. cyrtopsis* have a stripe like *e. eques*, so the ventral count must be relied upon to dis-

tinguish the two races.

Very rarely do 7 supralabials occur in *e. cyrtopsis*, while in *e. eques* 7 occur as frequently as 8.

The range of *e. cyrtopsis* in Mexico is the eastern half of Sonora southward to northern Durango and along the Sierra Madre Occidental to northern Nayarit; eastward through Chihuahua to eastern Coahuila, and southward on the central plateau to southern San Luis Potosí and probably northern Zacatecas.

Specimens of this race have been examined from the following localities. *Chihuahua*: Arroyo del Alamos, Casas Grandes (No. 42876); Basuriachi (FMNH No. 11823); Cajón Bonito Creek (No. 21056); Chihuahua (No. 14256); Guadalupe y Calvo (No. 46356-8); Mojarachic (EHT-HMS Nos. 18962-3, 23063-6, 23787); San Luis Mts. (Nos. 21057-8); Samachique (FMNH Nos. 11822, 11824, 15727). *Coahuila*: 21 miles north of Saltillo (No. 105303); Rinconada (No. 8067, type *cyrtopsis*). *Durango*: Guanacevi (No. 46367). *Nayarit*: Santa Teresa (Nos. 46420-1). *San Luis Potosí*: Hacienda La Parada (No. 46410). *Sonora*: La Posa, 10 miles north of Guaymas (EHT-HMS Nos. 4866-73); Guadalupe Cañon (No. 21059).

Scale Counts of *eques cyrtopsis*.

Museum	Number	Sex	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.	State
FMNH	11823	♀	170	—	8-8	10-10	1-1	2-3	Chih.
USNM	46356	♀	175	81	7-8	10-10	1-1	3-3	"
EHT-HMS	23063	♀	169	84	8-8	10-10	1-1	3-3	"
"	23065	♀	176	95	8-8	10-10	1-1	3-3	"
"	23066	♀	168	86	8-8	11-12	1-1	3-4	"
"	23787	♀	174	90	8-8	11-11	1-1	3-3	"
USNM	21058	♀	167	85	8-8	9-10	1-1	2-2	"
"	46367	♀	172	88	8-8	10-10	1-1	2-3	Dgo.
"	46420	♀	172	84	7-7	10-10	1-1	3-3	Nay.
"	46421	♀	166	84	7-7	10-10	1-1	3-3	"
EHT-HMS	4866	♀	163	78	8-8	10-10	1-1	3-3	Son.
"	4872	♀	171	86	8-8	10-10	1-1	2-2	"
"	4873	♀	166	77+	8-8	10-10	1-1	3-3	"
USNM	42876	♂	177	91	8-8	10-11	1-1	3-3	Chih.
"	21056	♂	169	94	8-8	10-10	1-1	3-3	"
"	14256	♂	172	102	8-8	10-10	1-1	3-3	"
"	46357	♂	174	92	8-8	10-10	1-1	3-3	"
"	46358	♂	174	—	8-8	10-10	1-1	3-4	"
EHT-HMS	18962	♂	174	89	8-8	10-10	1-1	3-3	"
"	18963	♂	169	99	8-8	10-10	1-1	3-3	"
"	23064	♂	173	98	8-8	10-10	1-1	3-3	"
USNM	21057	♂	173	91	8-8	10-10	1-1	3-3	"
FMNH	11822	♂	174	92	8-8	10-10	1-1	3-3	"
"	11824	♂	177	95	8-8	10-10	1-1	3-3	"
"	15727	♂	163	—	—	—	—	—	"
USNM	105303	♂	169	89	8-8	10-10	1-1	3-3	Coah.
"	8067	♂	173	88	8-8	11-11	1-1	2-3	"
"	46410	♂	174	91	7-8	10-10	1-1	3-3	S.L.P.
EHT-HMS	4867	♂	172	91	8-8	11-11	1-1	3-3	Son.
"	4868	♂	169	88	8-8	10-11	1-1	3-3	"
"	4869	♂	163	84	8-8	10-11	1-1	3-3	"
"	4870	♂	171	—	9-10	9-10	2-2	3-3	"
"	4871	♂	172	—	8-8	11-11	1-1	3-3	"
"	21059	♂	164	93	8-8	10-10	1-1	3-4	"

***Thamnophis eques postremus***  
subsp. nov.

*Type.* E. H. Taylor-H. M. Smith Coll. No. 5275, El Sabino, Michoacán, collected by H. M. Smith. *Paratypes.* Three, Nos. 5274, 5285-6, Uruapan, Michoacán.

*Diagnosis.* Similar to *e. eques*, except ventrals fewer, 138 to 141 in the only specimens known (4 females); caudals 71 to 72; supralabials 7 to 8; lateral light stripes not apparent; middorsal stripe but very little lighter than ground color, scarcely or not evident; dark spots very much reduced, alternating with each other in two series on either side; middorsum not traversed by spots; outer row of dark spots on first and second scale rows greatly reduced, generally scarcely visible; no distinct dark spots on venter.

*Description of Holotype.* Length of portion of rostral visible from above a little more than half length of median suture between internasals; latter a little longer than prefrontals, but much narrowed anteriorly, their combined width anteriorly somewhat less than a third the length of the posterior border of the rostral; frontal pentagonal, anterior edge straight, posterior edges forming an obtuse angle of about  $110^{\circ}$ ; length of frontal subequal to its distance from tip of snout and from posterior tip of parietals; nasal divided, nostril largely in anterior section and bordering posterior section; loreal large, nearly square; a large preocular, rather widely separated from frontal; three postoculars, upper a little the largest, lowest smallest and wedge-shaped; temporals 1-3-3, the primary much the largest. Supralabials 7-7, 5th largest, 3d and 4th entering orbit; infralabials 10-10, 5 bordering anterior chinshields, two (5th and 6th) bordering posterior chinshields; length of suture between 1st infralabials subequal to length of mental; anterior chinshields a little shorter and a little broader than posterior chinshields; latter separated from each other their full length.

Dorsal scales in 19-19-17 rows, strongly keeled, those in outer row with relatively weak keels; apical notches present on dorsal scales, but no typical apical pits; ventrals 139; caudals 72; total length 575 mm.; tail

144 mm.; female.

Maxillary teeth 27.

Dorsal surface of head slate gray, unmarked; sides of head the same color, becoming cream at labial border, but posterior borders of all labials with a distinct vertical black streak, most prominent on 5th labial; nape with a large black blotch fading anteriorly into the slate color of head, posteriorly sharply terminating about six scale lengths from edge of parietals; nape spot extending slightly below level of angle of mouth, and somewhat indented on middorsal line.

Ground color of body slate gray, a little lighter than head color; a poorly defined, short area cream in color immediately posterior to dark nuchal spot; a very feebly defined light line on vertebral scale row, very slightly lighter than ground color and lacking darker edges; lateral light stripes not visible but their position on the second and third scale rows indicated by the restriction of dark marks to areas lateral and medial to these rows. Sides of body with two series of small, poorly outlined but distinct, alternating black spots widely separated from each other and not encroaching whatever on the vertebral line or upon the second or third scale row; on the outer, anterior edges of certain scales of the outer row of dorsals is a small black spot; these tend to occur on alternate scales.

Venter cream, immaculate save for a small dark streak near either end of each ventral, placed on the anterior edge and concealed by the overlapping edge of the preceding scale; these small dark marks not visible except when scales are spread apart; chin and gular region cream, unmarked save for a dark streak on the posterior border of a few of the posterior infralabials; subcaudal surface immaculate.

*Variation.* One of the paratypes is marked exactly like the holotype. Another (No. 5286) has somewhat larger dark spots on the dorsal surface; the corners of the spots nearly touch on either side, but in no case do the spots cross the middorsal line; those in the paravertebral series alternate with each other. The last specimen, a juvenile, agrees with No. 5286 in pattern.

Variation in Scale Counts of *eques postremus*.

Number	5275	5274	5286	5285
Sex	♀	♀	♀	♀
Dorsals	19-19-17	19-19-17	19-19-17	19-19-17
Ventrals	139	138	140	141
Caudals	72	71	72	72
Supralabials	7-7	7-7	8-8	7-7
Infralabials	10-10	10-10	10-10	10-10
Preoculars	1-1	1-1	2-2	1-1
Postoculars	3-3	3-3	3-3	3-3
Temporals	1-3-3	1-3-3	1-3-3	1-3-3
Total length (mm.)	575	571	441	192
Tail length (mm.)	144	141	105	47

In the specimen with 2-2 preoculars the normal preocular is split across the middle; it is a type of anomaly not infrequent in *eques* and its relatives.

*Remarks.* In the low ventral count, *e. postremus* is like *s. sumichrasti*, *s. praeocularis*, *s. fulvus* and perhaps *s. cerebrosus*. The last and *s. praeocularis* have distinct spots on the belly and distinct, broad vertebral light stripes. In *s. sumichrasti* there is a median series of dark spots alternating with a series of lateral spots, as in *vicinus*. The closest resemblance to *s. postremus* of all these is held by *s. fulvus*, which also lacks belly spots and distinct stripes. In it, however, the middorsal stripe is visible, distinct and relatively broad (one and two half rows to three full rows) on the anterior part of the body, and becomes narrower posteriorly, disappearing completely on the posterior part of the body. In *e. postremus* the dorsal stripe is restricted completely to one scale row (as in *e. eques*) and is of equal indistinctness throughout its length.

***Thamnophis sumichrasti sumichrasti*  
(Cope).**

This form is characterized by the absence of a dorsal stripe, presence of a medial series of dark spots, a very poor definition of the lateral light stripes, and by having 19 scale rows and 139 to 157 ventrals, 58 to 72 caudals. In form, scutellation and type of pattern it is undoubtedly a close relative of *eques*, which differs by having a distinct dorsal stripe and higher average ventral and caudal counts. The two are considered as distinct species because there is no evidence whatever of an intergradation between the curious pattern of *sumichrasti*—a median and two lateral series of spots—with that of *eques*, which has a median light stripe and four lateral series of spots. *T. sumichrasti* does intergrade with races which do have patterns similar to that of *eques* (*viz.*, *s. fulvus*, *s. praeocularis*), but from that fact it cannot be inferred that *sumichrasti* must also intergrade with *eques*. For some time I labored under such an inference, but the discovery of *vicinus* has made it evident that intergradation between forms with patterns as different as those of *sumichrasti* and *eques* is not to be taken for granted. *T. vicinus*, with a pattern like *sumichrasti* but with a ventral count

like *eques*, occurs in the same localities as the latter species, yet remains quite distinct. Since it is so close a parallel of *sumichrasti* (differing chiefly in ventral count), I believe it unwise to assume that the latter is a subspecies of *eques*, any more than is *vicinus*.

Thus it appears that there are two centers of dispersal of the complex *eques* group: one in Guatemala, the other in Mexico. The most primitive of the groups may be *vicinus* and *s. sumichrasti*, respectively, each of which has given rise to striped forms some of which closely parallel each other (*e.g.*, *e. postremus* and *s. fulvus*). The chief difference between the history of the forms developing from these two centers of dispersal is that *vicinus* has become completely distinct from its striped derivative, *eques*, while *sumichrasti* still remains linked with its striped derivatives. Chiapas specimens of *sumichrasti* show definite evidence of intergradation of that form and *s. fulvus*.

In spite of evidence of separate centers of dispersal for *sumichrasti* and *eques*, the two species obviously have had a common origin, and *chrysocephalus* seems very near the ancestral type from which they were derived. *T. chrysocephalus* shows a strong similarity to *vicinus*, differing chiefly in number of scale rows and maxillary teeth.

The two cotypes of *sumichrasti* are very small and soft. They completely lack stripes, however, and have a series of spots crossing the vertebral scale row. Moreover they have 19 scale rows (19-19-17) and the low ventral and caudal counts typical of the subspecies. They may actually have been secured near Orizaba, as stated by Cope, but it appears more probable that they were collected on the Isthmus of Tehuantepec, on the Atlantic slopes. At best the locality data cannot be relied upon until verified by further specimens from the region of Orizaba, for in numerous instances the data for *Sumichrast's* specimens are known to have been misrepresented.

The name *sumichrasti* has previously been applied to a 17-scale-rowed form (*chrysocephalus* + *scalaris godmani*) and for this reason Dunn and I nearly simultaneously applied different names to the stripeless, 19-scale-rowed form to which actually belongs the name *sumichrasti*. These three names (*sumichrasti*, *bovalli*, *rozellae*) clearly refer to the same form.

Scale Counts of *s. sumichrasti*.

Museum	Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.
USNM	25234	♀	19-19-17	149	66	8-8	10-10	1-1	3-3
USNM	26501	♂	19-19-17	157	63	8-8	9-9	1-1	3-3
USNM	26502	♂	19-19-17	148	68	8-8	8-8	1-1	3-3
USNM	46549	♀	19-19-17	139	72	8-8	9-10	1-1	3-3
USNM	108597	♀	19(20)-19-17	140	58	7-7	9-9	1-1	3-4
USNM	108598	♂	19-19-(15)17	148	—	8-8	9-9	1-1	3-3
USNM	108599	♂	19-19-15	151	—	7-7	9-9	1-1	3-4

The localities now represented by specimens are: *Tabasco*: Montecristo (USNM No. 46549). *Veracruz*: ?Orizaba (USNM Nos. 26501-2). *Chiapas*: Palenque (USNM No. 108597); Aguacate, 24 kilometers north of Palenque (USNM No. 108598-9). *Guatemala*: (USNM No. 25234). *Nicaragua*: Granada (Dunn, *loc. cit.*)

***Thamnophis sumichrasti praeocularis*  
(Bocourt).**

The types of *praeocularis* are described with 140 ventrals, 68 to 74 caudals, and 19 scale rows. The type of *arabdotus* (FMNH No. 26994) has 140 ventrals, 72 caudals, and 19-19-17 scale rows (female). Two females in the U. S. National Museum (Nos. 46528-9) from Puerto Morelos, Yucatán, have 137 and 136 ventrals, respectively; caudals 70, 71; scale rows 19-17-15, 19-19-16. The patterns in all these specimens are remarkable alike, including a very broad median stripe; large nuchal blotches followed by smaller blotches on the body, of which a few anterior are fused to form single lateral cross-bands; and a series of black spots on each side of venter, a spot to the side of each ventral. This uniformity in pattern, as well as in most features of scutellation, leads me to believe that the presence of three preoculars in the types (both?) of *praeocularis* is an anomaly; there is no other feature which could distinguish them from *arabdotus* as another species or subspecies.

***Thamnophis sumichrasti cerebrosus*\*  
subsp. nov.**

*Holotype*. U. S. Nat. Mus. No. 12734, female, Escuintla, Guatemala, collected by H. J. Stuart. *Paratypes*. U. S. Nat. Mus. No. 12735, topotype; F.M.N.H. No. 410, "Guatemala."

*Diagnosis*. Dorsal stripe covering one and two half scale rows, with continuous lateral edges; lateral stripe poorly defined or absent; two regular rows of dark spots on venter, at least toward posterior part of belly; head light above, with discreet vertical dark marks on edges of supralabials; ventrals 144 to 167. Scale rows regularly 19-19-17.

*Description of Holotype*. Internasals a little shorter than wide, their combined contact with rostral considerably greater than a nasorostral suture; prefrontals a little longer than internasals; frontal very slightly shorter than its distance from tip of snout or length of parietal suture; greatest width of frontal four-fifths its length, least width about half its length; one loreal, about as high as long; a large preocular; three post-

oculars, lower smallest; temporals 1-3, anterior very large; supralabials 7-7, 3d and 4th entering eye, 5th highest and largest; ten infralabials, five in contact with anterior chinshields, two with posterior; posterior chinshields separated from each other, a third longer than anterior chinshields.

Dorsal scales in 19-19-17 rows, all strongly keeled except those of outer row, which are weakly keeled; ventral 144; anal divided; subcaudals 66 (female).

Head very light brown; two small, white pineal spots; posterior edges of 2d to the 5th supralabials inclusive black-edged, the anterior scales less prominently; otherwise head without markings. Two dark nuchal blotches partially fused medially; a very distinct, sharply outlined middorsal light stripe covering one and two half scale rows, extending from nape onto tail; below this two series of alternating spots on each side, the lower reaching to and including the upper part of the third scale row; irregular dark areas on many scales of the three outer rows. Belly light, with small, black spots near the anterior end of each ventral, arranged in a series on each side, near ends of ventrals; other scattered dark spots and irregular dark areas near bases of many ventrals, especially those near middle of body; chin with a very few, tiny dark flecks below.

*Variation*. The topotypic paratype has an anomalous pattern, and the head scutellation is not normal. Apparently it should have 7-8 supralabials, as the outlines of the scales indicate this number, but they are so fused that only six remain on each side. In scutellation it is otherwise normal, and has 10-10 infralabials, 1-1 preoculars, 3-3 postoculars, 19-19-17 scale rows, 149 ventrals and 74 caudals (male). The head shows no markings whatever. The body lacks all pattern characters save the middorsal stripe, which is narrower than in the type (involves only the edges of the paravertebral rows) and black-bordered; there are flecks of black on some lateral scales, and the nuchal blotches are indicated by black flecks on certain nuchal scales; the belly is unspotted.

The Field Museum paratype has 167 ventrals, 78 caudals, 7-7 supralabials, 10-10 infralabials, 1-1 preoculars and 19-19-17 scale rows. It is like the holotype, except that the pattern is less well defined (scales not spread apart as in holotype); the anterior spots are fused together, reproducing more or less the lateral neck pattern of *praeocularis*; and the rows of spots on the belly are shorter and the spots smaller.

*Comparisons*. This form appears to be most closely related to *praeocularis*, having

\* *Light-headed*, in reference to the relatively light ground color and poorly defined dark marks on head.



a very similar body pattern. The most distinctive pattern differences are found on the head. In *praeocularis* the dorsal surface of the head is dark, the lips are strongly barred, and the nuchal blotches are fused with the head color. The ventrals are a little less numerous than in *cerebrosus*, varying from 136 to 140 in four specimens (females). Whether there will prove to be average differences in neck pattern cannot now be stated; in *praeocularis* the first few body spots are single, instead of double and alternating, and cross the lateral light stripe; this pattern does not occur in the type of *cerebrosus*, but does in the single normal paratype. It is also possible that the number of supralabials in *cerebrosus* may average fewer than in *praeocularis*.

***Thamnophis sumichrasti fulvus***  
(Bocourt).

This rather well-defined form is characterized by the indistinctness of the dorsal stripe, which is poorly defined and about one scale row wide (except sometimes on the neck); the head generally is light, and always with no or very discreet dark labial marks; dark marks on the belly, as in *praeocularis* and *cerebrosus*, are completely lacking; scale rows 19–19–17 (a short row medially on each side, increasing the count to 21, in one specimen out of 32; one other specimen with 15 posteriorly); supralabials regularly 8–8; ventrals 136 to 153; caudals 58 to 76.

The subspecies is known only from central Guatemala. Specimens examined are from Sierra Santa Elena, Tecpam, 9500 ft. (FMNH Nos. 1926, 30432–3) and Chichivac, Chimaltenango (FMNH Nos. 20261–2, 20275). Slevin (Proc. Calif. Acad. Sci., ser. 4, vol. 23, 1939, p. 397) records 26 specimens from Chichivac, in the vicinity of Tecpam (CAS Nos. 66983–98); Lake San Antonio, near San Antonio (CAS Nos. 66983–98); and Finca El Potrero, Volcán Agua (CAS No. 66973). The race may exist in Chiapas. Apparently it occurs only at relatively high elevations, while *cerebrosus* and *praeocularis* are lowland and foothill subspecies.

The closest relative of *fulvus* is not *praeocularis* or *cerebrosus*, which are closely associated geographically, but more probably *sumichrasti*. With the latter *fulvus* agrees in head pattern (no dark labial marks), ventral pattern (no spots) and in scale counts; the only significant difference between these two is in the presence of stripes (although dim except on neck) in *fulvus*, the absence of them in *sumichrasti*. This difference, though slight, is very constant in the specimens examined.

***Thamnophis ordinoides errans***  
subsp. nov.

*Holotype*. USNM No. 46336, female, from Colonia García, Chihuahua. *Paratypes*. Three topotypes, Nos. 46337–9, and two from Coyotes, Durango (FMNH Nos. 1499A–B).

*Diagnosis*. A member of the *ordinoides* group, with 19–19–17 scale rows and maxillary teeth 17 or 18, the posterior not conspicuously enlarged, although a little longer than the anterior teeth; ventrals 155 to 166 (155–156, females; 163–166, males); caudals 72 to 91 (72 to 82, females; 85 to 91, males); supralabials seven or eight; sixth labial large and not narrowed above; stripes very poorly defined as a rule, median stripe generally covering but one scale row where visible; spots between stripes small, those of the outer row usually very poorly defined or absent; top of head dark, the color extending onto sides; supralabial region light, except for black posterior edges on most of the labials; a vaguely darker, longitudinal line through lower temporal region.

*Description of Holotype*. Portion of rostral visible from above as long as internasal; suture of one of latter with rostral as great as naso-rostral suture, or a little longer; one preocular; three postoculars; temporals 1–2–3; eight supralabials on one side, on the other side the two subocular labials fused; anterior and posterior edges of 6th labial parallel, inclined forward slightly; 6th labial a little higher than long; ten infralabials; posterior chinshields separated from each other, a little longer than anterior chinshields.

Scale Counts of *s. fulvus*.<sup>3</sup>

Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.
20261	♂	19–19–15	146	69	8–8	10–10	1–1	3–3
20262	♂	19–19–17	145	75	8–8	10–10	1–1	3–3
1926	♀	19–19–17	136	—	8–8	9–10	1–1	3–3
20275	♀	19–19–17	142	60	8–8	10–11	1–1	3–3
30432	♀	19–19–17	144	59	8–8	10–10	1–1	3–3
30433	♀	19–21–17	142	58	8–8	10–11	1–1	3–4

<sup>3</sup> See Slevin (*loc. cit.*) for counts on the 26 specimens in the California Academy of Sciences.



Scale rows 19-19-17, the fourth row dropping at the 104th ventral; ventrals 156; anal entire; caudals 82, total length 545 mm.; tail 139 mm.

Dorsal surface of head uniform dark brown, the color extending onto sides, without marks; labial region cream; an area on posterodorsal edge of labials (except last) black; loreal, nasal, two lower postoculars and lower half of preocular suffused with cream; temporal region dark, nearly black at sutures with labials, abruptly differentiated from light labial color; posterior to temporal region and parietals, the brown color of head shades into a black nuchal patch extending posteriorly four scale lengths, this patch extending laterally a little below angle of mouth, and sharply differentiated posteriorly and below from the adjacent light color. Dorsal ground color brown, lighter brown below middle of third and on vertebral scale rows; on neck a single, poorly defined series of transversely elongate spots; this series breaks into two rows, and the lower of these rows disappears on anterior fourth of body; the median series of spots continues about to middle of body, there disappearing; on posterior third of body no markings whatever are visible, and only the lighter ground color below the middle of the third row indicates the position of the lateral light stripe. Tail uniform brown. Chin and gular area cream, unmarked; otherwise entire ventral surface slate gray, the posterior edges of the scales light.

Variation. In coloration the subadult male and one juvenile topotype are just like the holotype; the other juvenile topotype has the spots in the outer row more clearly defined, visible (though dimly) to the tail. All agree with the type in having the nasorostral suture much smaller than the combined internasal-rostral sutures.

The two paratypes from Coyotes, Durango, differ in coloration from the topotypes only in the greater distinctness of the dorsal stripe. In the larger the stripe is distinct the full length of the body, and involves the inner halves of the paravertebral scale rows; it divides the nuchal blotches and reaches the parietals. In the smaller

specimen the stripe is only one scale row wide, but it is distinct posteriorly as well as anteriorly. There are no markings below the vaguely indicated lateral light line.

Remarks. These are the first specimens recorded from mainland Mexico (i.e., exclusive of Baja California) of the *ordinoides* group. They differ from all except *ordinoides*, *atratus*, and *hydrophila* by having a maximum of 19 scale rows. Of these, *ordinoides* has fewer ventrals and caudals; *atratus* has a distinct dorsal stripe and frequently has red in the dorsal color; and *hydrophila* regularly has eight labials, the sixth narrower above than below, and the combined internasal-rostral sutures less than a single naso-rostral suture (these characters from Fitch, *Univ. Calif. Publ. Zool.*, vol. 44, 1940).

Of known Mexican species, the one most easily confounded with *errans* is *eques eques*, a form having similar scutellation at least in the southern part of its range. The latter may be distinguished by the presence of dark spots below the lateral light line (on the scales); by the distinct lateral light line; and by the number and character of the maxillary teeth. Two *eques eques* examined (from the states of Sonora and Mexico) have 24 and 26 maxillary teeth, and the last is much larger (two or three times) than the anterior and middle teeth. Two *errans* (one from each locality) have 17 and 18 maxillary teeth, and the posterior is but little larger than the middle and anterior teeth; these maxillae resemble one extracted from a specimen of *ordinoides vagrans* from Rinconada, New Mexico (USNM No. 44361), with 20 teeth, the last but little enlarged.

The relationships and phylogenetic position of *errans* are not clear, and cannot well be guessed until more specimens show the type of variation that exists in it. The resemblance to *eques* is so close that the possibility of its derivation from the latter should be considered; if such is the case, then *errans* would have to be looked upon as the most primitive of the *ordinoides* group; this is the view here considered the most probable. According to Fitch's theories,

Scale Counts in *ordinoides errans*.

Number	46336	46339	46337	46338	1499	1499
Sex	♀	♀	♂	♂	♂	♂
Scale Rows	19-19-17	19-19-19	19-19-17	19-19-17	19-19-17	19-19-17
Ventrals	156	155	166	163	156	158
Caudals	82	72	91	85	90	91
Supralabials	8(7)-8	7-8	7-7	7-7	7-7	7-7
Infralabials	10-10	10-11	10-10	10-11	10-10	10-10
Preoculars	1-1	1-1	1-1	1-1	1-1	79
Postoculars	3-3	3-3	3-3	3-3	3-3	1-1
Total length (mm.)	545	214	437	242	610	2-2
Tail length (mm.)	139	51	117	68	159	300

however (and *Ruthveni's*), *errans* probably would be considered one of the end forms of the artenkreis, paralleling the *ordinoides* section in its reduced scutellation and broad snout.

***Thamnophis sirtalis parietalis* (Say).**

A specimen collected by Nelson and Goldman at Casas Grandes, Chihuahua (USNM No. 46371), is the only specimen of this species known from Mexico. It is a female with 19-19-17 scale rows, 152 ventrals, tail incomplete, supralabials 7-7, infralabials 10-11, preoculars 1-1, postoculars 3-3. The spots in the upper row are fused together, and those in the lower row are confluent with the upper row but not with each other; the spaces between the latter are red.

***Thamnophis marcianus*  
(Baird & Girard).**

This species is characterized by having a distinct lateral light stripe confined to the third row of scales; the only other having a similar disposition of the lateral stripe is *ruthveni*. In the latter, however, the mid-dorsal stripe involves only the vertebral scale row; in *marcianus* it covers the adjacent halves of the paravertebral rows as well. In addition the ventrals in *ruthveni* are generally fewer.

In body pattern, particularly in the neck region, this species as well as *ruthveni* shows a much greater similarity to the *eques* group than it does to *megaloops*.

The forty-seven specimens examined are from the following localities: *Sonora*: (No. 7235); *Chihuahua*: Ojos del Diablo, Santo Domingo Ranch (No. 30837); 16 leagues north of Guerrero (No. 46583); 10 miles north of Ciudad Delicias (No. 105293); Progreso (near Casas Grandes) (Nos. 104634-41); 5 miles south of Ciudad Juárez

(EHT-HMS No. 5418); Río San Pedro, betw. Chihuahua City and Naica (EHT-HMS Nos. 5319-22, 5419, 5421-3). *Durango*: 5 miles north of Conejos (EHT-HMS No. 5420); between Lerdo and La Goma (No. 109295). *Coahuila*: 2-3 miles east of Torreón (EHT-HMS No. 4996); Santa Helena Canyon, Río Grande (FMNH No. 26135). *Nuevo León*: Mamulique Pass (EHT-HMS No. 5287); Sabinas Hidalgo (EHT-HMS No. 28653); 8 miles W. of Monterrey (EHT-HMS No. 23615). *Tamaulipas*: Matamoras (Nos. 861, 5491, 15344); Charco Escondido (No. 1849); Rancho El Plato, 38 miles southeast of Reynosa (No. 95183). Garman (*Bull. Essex Inst.*, vol. 19, 1887, pp. 7-8) records the species from "San Luis Potosí," but the record appears to be in error.

***Thamnophis ruthveni* Hartweg & Oliver.**

Similar to *marcianus*, having the lateral stripe confined to the third scale row, but differing in having a narrow middorsal stripe covering only the vertebral scale row (one and two half rows in *marcianus*), and generally by having fewer ventrals (147 to 154 in males, 141 to 150 in females; *marcianus* has 151 to 165 in males, 144 to 159 in females). It is known only from the Pacific side of the Isthmus of Tehuantepec, where it has been taken near Tehuantepec, at Chivela, and at San Mateo del Mar, state of Oaxaca.

Two specimens examined are from Tehuantepec (No. 110802) and Chivela (No. 46364). Both are males, and respectively have 21-21-17, 21-21-16 scale rows; ventrals 153 in both; caudals ?, 71; supralabials 8-8, infralabials 10-10, preoculars 1-1, postoculars 4-4, a minute anterior temporal in each. Three other specimens (EHT-HMS Nos. 27562-4) are from Tehuantepec.

**Scale Counts of *marcianus*.**

Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.
28653	♀	21-21-17	150	65	8-8	10-10	1-1	4-4
5491	♀	21-21-17	146	—	8-8	10-10	1-1	3-4
849	♀	21-21-17	144	—	8-8	10-?	1-1	4-4
7235	♀	21-21-17	153	67	8-8	10-10	1-1	4-4
26135	♀	21-21-17	150	—	8-8	10-11	1-1	3-3
30837	♀	21-21-17	150	—	8-8	9-10	1-1	4-4
46583	♀	21-21-17	148	—	8-8	10-10	1-1	4-4
104635	♀	21-21-17	157	66	8-8	9-10	1-1	3-3
104637	♀	21-21-17	154	62	8-8	9-9	1-1	3-3
104639	♀	21-21-17	156	—	—	—	—	—
104640	♀	21-21-17	156	—	8-8	9-10	1-1	3-3
104641	♀	21-21-17	156	—	8-8	9-10	1-1	3-4
105293	♀	21-21-17	155	69	8-8	10-11	1-1	3-4
105295	♀	21-21-17	154	—	8-8	10-10	1-1	3-4
15344	♂	21-21-17	151	76	8-8	10-10	1-1	3-4
95183	♂	21-21-17	153	78	8-8	9-10	1-1	4-4
104634	♂	21-21-17	162	—	7-8	10-10	1-1	4-4
104636	♂	21-21-17	165	72	8-8	10-10	1-1	4-4
104638	♂	(19)21-21-17	160	70	8-8	9-9	1-1	3-4

# *Thamnophis macrostemma macrostemma* (Kennicott).

As stated previously (Smith, *Zool. Ser. Field Mus. Nat. Hist.*, vol. 24, 1939, pp. 29-30), this species cannot stand as *megalops*; if the latter name is to be used, it must be for a subspecies of *macrostemma* (since it is not based upon a distinct species) for Cope (*Bull. U. S. Nat. Mus.*, No. 1, 1875, p. 41) chose the latter as the name for the species.

It seems that *macrostemma* is composed of one or more populations differing to some extent from each other. Nevertheless I am not certain that the differences previously pointed out by me (*loc. cit.*) between northern and southern specimens actually differentiate two populations, instead of merely expressing a lack of specimens from territories intervening between the two geographical extremes. Specimens from certain localities in such intermediate territory which have been studied more recently do turn out to be intermediate, and thus is supported a possibility that the variation in ventral and caudal counts exhibits a definite south-north trend independent of the variation in other characters, such as color, that may actually define several true populations in the species. That color characteristics may define geographic races in this species has been emphasized by Ruthven (*op. cit.*) and more recently by Brumwell (*Trans. Kans. Acad. Sci.*, vol. 42, 1939 [1940], pp. 423-429, pl. 1). The difficulty of analyzing color differences upon the basis of only preserved specimens has made impractical a further study of this aspect of the problem at the present time.

However, despite certain doubts in my own mind of the validity of such a separation, the recognition of a northern and a southern race of *macrostemma* based upon differences in ventral and caudal counts is still statistically sound.

In caudal counts of males, 93% of *m. macrostemma* have 78 or less, while 91% of *m. megalops* have 79 or more; in females 94% of *m. macrostemma* have 68 or less, while 95% of *m. megalops* have 69 or more. In ventral counts of females 85% of *m. macrostemma* have 185 or less, while 54% of *m. megalops* have 159 or more; the over-

lap in males is practically complete. In total counts of males, 86% of *m. macrostemma* have 242 or less, while 95% of *m. megalops* have 243 or more; in females of *m. macrostemma*, 79% have 225 or less, while in *m. megalops* 89% have 226 or more.

Specimens recently examined add further data for the table of variation previously published.

The following distributional records are available. *Nayarit*: Santa Teresa; Tepic. *Jalisco*: Atemajac; Chapala; 20 km. south of Guadalajara; Guadalajara; La Quemada; Magdalena; Ocotlán. *Michoacán*: Lake Cuitzeo; Pátzcuaro; Zamora; Tacicuaró. *México*: Chalco; Chimalhuacán; Lerma; San Pedro Tultepec; Toluca; Nevado de Toluca; 7-10 miles west of Villa Victoria. *Distrito Federal*: Chapultepec; Coyoacán; La Viga Canal; Mexico City; Xochimilco. *Puebla*: Atlitico; Puebla; Tecamachalco. <sup>4</sup>*Veracruz*: Acateño; Mirador; Orizaba. *Oaxaca*: Mitla.

The specimens from the vicinity of Lake Chapala and La Quemada are intermediate in character between the two races, and were not included in the comparisons given above. For data on variation in these specimens see Brumwell, *op. cit.*

# *Thamnophis macrostemma megalops* (Kennicott).

The following distributional records in Mexico are available. *Chihuahua*: Chihuahua; Colonia Juárez; Jiménez; Miñaca; San Andrés; Río San Pedro between Naica and Chihuahua City; Progreso, near Casas Grandes (on Río Santa María); Casas Grandes; Colonia García; Santa Rosalia; Sierra Madre. *Sonora*: Santa Magdalena (Tuscon Ariz.?). *Durango*: Ada Magdalena; Coyotes; Durango; El Salto; Río Tunal, above Pueblito; Lerdo. *San Luis Potosí*: Hda. La Parada. *Guanajuato*: Guanajuato; Irapuato; Moro León; Salamanca; Tupátaro (this may be one of the towns of the same name in the state of Michoacán); Celaya. *Hidalgo*: La Vega, Mizquiahuala, Valle de Mezquital (Martín del Campo, *Anal. Inst. Biol. Mex.*, vol. 8, 1937, p. 264).

<sup>4</sup> Localities in this state probably incorrect.

## Variation in Scale Counts of *Thamnophis macrostemma*.

Race	Sex	Caudals			Ventrols			Totals		
		No. Spec.	Range	Av.	No. Spec.	Range	Av.	No. Spec.	Range	Av.
<i>m. megalops</i>	♂	23	77-89	82	32	159-172	165	20	242-255	248
<i>m. megalops</i>	♀	22	68-89	74	30	149-164	157	18	222-260	235
<i>m. macrostemma</i>	♂	43	65-81	74	53	129-169	164	42	226-245	237
<i>m. macrostemma</i>	♀	33	61-71	66	48	150-171	158	33	210-228	221

***Thamnophis sauritus proximus* (Say).**

Mexican specimens examined since 1938 (Smith, *Occ. Papers Univ. Mich. Mus. Zool.*, No. 388, 1938, pp. 5-7) are from 60 miles south of Matamoras, Tamaulipas (FMNH No. 27183); Hda. La Clementina, Tamaulipas (No. 105305); and Acultzingo, Veracruz (Nos. 110803-4). These have 165, 160, 159, 160 ventrals, respectively; caudals 94+? (♂), 102+ (♂), 97 (♂), 98 (♀). The Acultzingo record must represent nearly the extreme southern edge of the range of the subspecies, as at about the same parallel *chalceus* occurs on the coast.

***Thamnophis sauritus chalceus* (Cope).**

The range of this subspecies is from central Veracruz to Costa Rica. To the localities mentioned by Dunn (*Herpetologica*, vol. 1, 1940, pp. 192-3) and Smith (*op. cit.*, pp. 5-6, pl. 1) can be added Jonuta (No. 110805) and Montecristo (No. 46584), *Tabasco*; Puerto Morelos (No. 46530) and Cozumel Island (No. 13906), *Yucatán*; Cobá (FMNH No. 26972), *Quintana Roo*; San Gerónimo (FMNH No. 1459), *Oaxaca*; and Potrero Viejo (EHT-HMS No. 5272), *Veracruz*.

***Thamnophis melanogaster melanogaster* (Peters).**

It seems not to have been generally recognized that eastern specimens of this very distinct species are the only ones with a broad, black area on the belly and tail; specimens from the western and northern parts of the range have a narrow, mid-ventral dark line frequently scarcely evident. The lateral light stripes are seldom not visible (placed on the second and third scale rows) in eastern specimens, but seldom evident in the western. Young, subadults and sometimes even large specimens of eastern specimens have a narrow, mid-dorsal light line involving only the vertebral scale row, while western specimens show no middorsal light line in either young or old. Moreover eastern specimens generally (81%) have the second labial in contact with the nasal on both sides of the head (usually the contact is broad), while in western specimens this occurs in but 22%. Eastern specimens also usually (75%) have 3-3 or more postoculars, while western specimens usually have 2-3 or 2-2 (72%). Finally, the caudals in eastern specimens are usually 64 or less in males (84%), 54 or less in females (73%), while in western specimens they usually number 65 or more in males (69%), 55 or more in females (84%).

The name *melanogaster* probably, although not certainly, is referable to the

eastern specimens. Peters' description is very brief and states only that a median black band is present on the belly, and that it is less distinct on the tail. The description might well apply to western specimens, but such a name as *melanogaster* hardly fits them, while it is very descriptive of the eastern specimens. Accordingly I restrict Peters' name to the eastern race, pending a study of the types that will definitely allocate the name.

*Tropidonotus mesomelanus* Jan also is based upon the eastern race as shown by the excellent figures on plates 5 and 6, livraison 27, of the *Iconographie Générale des Ophiidiens*. The pigmentation of the tail is less extensive than usual and the anal plate is unmarked in one of the figures (pl. 6), but I have seen a specimen from Lake Xochimilco which duplicates the pattern shown in the figure so exactly that I have no doubt in referring the specimen depicted to the eastern race. On plate 5 another specimen, this from the Vienna Museum, is figured; it is a very typical specimen of the eastern race, and is here designated lectotype of Jan's *mesomelanus*.

A final name synonymous with *melanogaster* is *Tropidonotus Baronis Mülleri* Troschel. This is synonymized with the typical race of *melanogaster* for several reasons. In the first place the name is not in binomial form, since the species name consists of two words. The name, thus written, cannot be accepted; had a hyphen been used, thus making one word of it, the form would satisfy requirements of binomial nomenclature. Boulenger, in fact, referring the name to the synonymy of *melanogaster* (*Cat. Snakes Brit. Mus.*, vol. 1, 1893, p. 226) hyphenated the name, thus giving it nomenclatorial status. His description is based upon specimens of both races of *melanogaster*; I restrict it to eastern specimens, referable to the typical race.

Troschel's description of *T. Baronis Mülleri*, moreover, is not certainly identifiable to subspecies; the specimens are, of course, definitely *melanogaster*, but whether eastern or western is not made evident. By inference, since a comparison is made with *T. grahamii* and the belly is stated to have a midventral dark streak like that species, Troschel's specimens may have been western, for the belly streak in *grahamii*, when present, is quite narrow as in western *melanogaster*. The identification at present however cannot be definite; fortunately this is not imperative since Troschel's name is not available.

Accordingly no name proposed in the past appears to be available for the widely-distributed western race. It is named and described in the following. If, however, at some future date it develops that Peters'

type of *melanogaster* is based upon western specimens, then his name must take precedence over the one proposed here, and *mesomelanus* Jan will be available for the eastern race. Unfortunately it is impossible at present to offer a more assuredly permanent nomenclature for these snakes.

In 31 specimens, 25 have the second labial in contact with the nasal on both sides, 4 on one side, 2 on neither side. In 44 specimens, the postoculars are 2-2 in six, 2-3 in five, 3-3 in thirty, 3-4 in three. The ventrals are 144 to 158 in males, average 148.3, in females 140 to 153, average 145.2. The caudals are 58 to 68 in males, average 62.3, in females, 50 to 61, average 53.5.

Specimens examined of *Thamnophis melanogaster melanogaster* are from the following localities. *Distrito Federal*: Mexico City (Nos. 12726, 12729); Lake Xochimilco (EHT-HMS No. 5063). *México*: Chalco

(FMNH Nos. 983, 1099, 2038); Chimalhuacán (Nos. 110793-8); Lerma (EHT-HMS Nos. 5044-62, 5075-8, 5076A, 15942-7). The only record in the literature for a locality not represented by specimens examined and probably referable to *m. melanogaster*, is Jicaltepec, Veracruz.

These records indicate a range from central México (state) to western central Veracruz; it possibly occurs also in northern Puebla and southern Hidalgo.

*Thamnophis melanogaster canescens*  
subsp. nov.

*Holotype*. EHT-HMS No. 5023, male, from Lake Chapala at Chapala, Jalisco, collected July 2, 1935, by H. M. Smith. *Paratypes*. Sixty-four, including EHT-HMS Nos. 4896, 4921, 4923-32, 4928A, 4934, 4936, 4939-41, 4942A, 4943, 4967-73, 4970A, 5020-2, 5024-43, all topotypes, same date and collector;

Scale Counts in *melanogaster melanogaster*.

Museum	Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.
FMNH	983	♀	19-19-17	145	61	8-8	10-10	1-1	3-4
"	2038	♀	"	153	55	8-8	10-10	1-1	3-4
"	1099	♀	"	153	57	8-8	10-10	1-1	3-3
"	1099	♀	"	147	—	8-8	9-10	1-2	2-3
USNM	12726	♀	"	150	51	8-8	10-10	2-3	3-3
"	12729	♀	"	150	59	8-8	9-10	2-2	3-3
"	110794	♀	"	150	—	8-8	10-10	1-2	2-2
"	110797	♀	"	150	53	8-8	10-11	2-2	2-2
EHT-HMS	5044	♀	"	143	53	8-8	10-10	2-3	2-2
"	5045	♀	"	143	51	8-8	10-10	2-2	3-3
"	5046	♀	"	141	51	8-8	10-11	2-2	3-3
"	5047	♀	"	141	52	8-8	10-11	2-2	3-3
"	5048	♀	"	142	53	8-8	9-10	2-3	3-3
"	5049	♀	"	144	54	8-8	10-10	2-2	3-3
"	5051	♀	"	143	52	8-8	9-10	2-2	3-3
"	5052	♀	"	141	55	8-8	9-10	2-2	3-3
"	5057	♀	"	143	52	8-8	10-10	2-2	2-3
"	5058	♀	"	141	54	8-8	10-10	2-2	2-2
"	5060	♀	"	143	52	8-8	10-10	2-2	3-3
"	5063	♀	"	145	57	8-8	10-10	2-2	2-2
"	15943	♀	"	140	51	8-8	10-11	2-2	3-3
"	15944	♀	"	146	52	8-8	10-10	2-3	3-3
"	15945	♀	"	142	—	8-8	10-10	2-2	2-3
"	15946	♀	"	146	53	8-8	10-10	2-2	3-4
"	15947	♀	"	147	50	8-8	11-11	2-2	3-3
FMNH	1099	♂	"	155	67	8-8	10-10	1-1	3-3
USNM	110793	♂	"	158	68	8-8	10-10	2-2	3-3
"	110795	♂	"	152	68	8-8	9-10	2-2	2-2
"	110796	♂	"	154	59	8-8	10-10	3-3	3-3
"	110798	♂	"	152	64	7-7	10-10	2-2	3-3
EHT-HMS	5050	♂	"	150	59	8-8	10-10	2-2	2-3
"	5053	♂	"	145	61	8-8	9-10	2-2	3-3
"	5054	♂	"	144	60	8-8	10-11	2-2	3-3
"	5055	♂	"	147	62	8-8	10-10	2-3	3-3
"	5056	♂	"	144	64	8-8	10-10	2-2	3-3
"	5059	♂	"	147	64	8-8	9-10	2-3	3-3
"	5061	♂	"	149	64	7-8	10-10	1-2	3-3
"	5062	♂	"	145	61	8-8	9-10	2-2	3-3
"	5075	♂	"	147	63	8-8	10-10	2-2	3-3
"	5076	♂	"	147	61	8-8	10-10	2-2	3-3
"	5077	♂	"	146	58	8-8	10-10	2-2	2-3
"	5078	♂	"	146	62	8-8	10-10	2-2	3-3
"	5076A	♂	"	145	59	8-8	10-10	2-2	3-3
"	15942	♂	"	146	59	8-8	10-10	2-2	3-3

EHT-HMS No. 5019, Magdalena, Jalisco; EHT-HMS Nos. 5064-5, Lake Cuitzeo, Michoacán; EHT-HMS Nos. 5066-71, three miles east of Celaya, Guanajuato; FMNH No. 1529(2), Ocotlán, Jalisco; USNM No. 110800, Tacicuaró, Michoacán; USNM No. 110799, La Palma, Michoacán.

*Diagnosis.* Like *Thamnophis melanogaster melanogaster*, except: belly with scattered spots, immaculate or, usually, a narrow, sometimes broken longitudinal midventral dark line; lateral light stripes rarely evident; subcaudal surface unmarked or with a narrow, irregular median streak; never a middorsal light line; second labial generally (78%) separated from nasal on one or both sides of head; postoculars generally (72%) 2-2 or 2-3; subcaudal scales generally (67%) 65 or more in males, 55 or more in females (84%).

*Description of Holotype.* Head narrow, somewhat pointed, lores somewhat flaring; length of rostral visible from above two-thirds length of suture between internasals; latter equal to length of suture between prefrontals; frontal pentagonal, anterior

edge straight, posterior edges forming a right angle, sides somewhat concave, very slightly narrower posteriorly than anteriorly; length of frontal subequal to length of suture between parietals, slightly less than distance from frontal to tip of snout; sutures between nasals and rostral three-eighths width of posterior margin of rostral; nasal completely divided, anterior section subequal in size to posterior; loreal large, rectangular, longer than broad; preocular single on one side, but a lower part partly divided by two incomplete sutures; preoculars two on other side, upper much the larger; postoculars 2-3; temporals 1-2-2.

Supralabials 8-8, second narrowly in contact with nasal on one side, narrowly separated on the other; seventh labial largest, fourth and fifth entering orbit; infralabials 10-10, five in contact with anterior chinshields, two (fifth and sixth) with posterior chinshields; latter a little longer and broader than anterior, separated from each other throughout their length, divergent posteriorly.

Dorsal scales in 19-19-17 rows, all except those in outer two rows keeled and truncate;

#### Scale Counts in *melanogaster canescens* (Males).

Museum	Number	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.
FMNH	1384	19-19-17	146	65	8-8	10-10	2-3	2-3
"	1384	"	149	67	8-8	10-10	1-1	3-3
"	1500	"	155	75	8-8	10-10	1-1	3-3
EHT-HMS	*4896	"	147	59	8-8	10-10	2-3	3-3
"	*4921	"	149	60	8-8	10-10	2-2	2-2
"	†4923	"	146	63	8-8	10-10	2-3	2-3
"	†4924	"	147	64	8-8	10-10	2-2	3-3
"	†4926	"	147	67	8-8	10-10	2-2	3-3
"	†4927	"	146	65	8-8	10-10	2-2	3-3
"	†4928	"	148	63	8-8	10-10	2-2	2-3
"	†4931	"	147	64	8-8	10-10	2-2	3-4
"	*4934	"	148	65	8-8	10-10	2-2	2-3
"	*4936	19-19-15	149	70	8-8	10-10	2-2	3-3
"	*4939	19-19-17	148	67	8-8	10-10	2-2	2-2
"	*4940	"	149	70	8-8	10-10	2-2	2-3
"	*4941†	"	147	67	8-8	10-10	2-2	2-2
"	4942A	"	145	63	8-8	10-10	2-2	2-2
"	4943	"	147	67	8-8	10-10	§1-1	2-2
"	4970	"	148	—	8-8	10-10	2-2	3-3
"	4970A	"	148	—	8-8	10-11	2-2	2-2
"	4973	"	149	72	8-8	10-10	2-2	2-3
"	5023	"	148	69	8-8	10-10	1-2	2-3
"	5024	"	148	68	8-8	10-10	§1-2	2-2
"	5027	"	145	69	8-8	10-10	2-2	2-2
"	5028	"	143	67	8-8	10-10	2-2	2-2
"	5029	"	144	65	7-7	10-10	2-2	2-2
"	5030	"	146	68	8-8	10-10	2-2	2-2
"	5032	"	148	67	8-8	10-11	2-2	2-3
"	5034	"	146	63	8-8	10-10	2-2	2-3
"	5066	"	151	71	8-8	10-10	2-3	2-2
"	5071	"	152	73	8-8	9-9	2-2	2-3
USNM	23985	"	144	—	8-8	10-10	3-3	3-3
"	23986	"	149	—	8-8	10-10	2-2	3-3
"	23987	"	145	61	8-8	10-?	2-2	2-3
"	46412	"	154	69	8-8	10-10	2-3	3-3
"	46413	"	149	70	7-7	9-10	2-2	2-2
"	46414	"	150	71	8-8	10-10	2-2	3-3

\* Young of No. 5038

† Young of No. 5021

‡ Anal divided

§ Loreal entering orbit.

scales in anal region with a central enlargement on the keel; ventrals 148; caudals 69; total length 525 mm., tail 124 mm.; male.

Entire dorsal surface slate (scales shed); when scales are spread, a narrow, interrupted, pure white line on the skin and adjacent edges of the third and fourth scale rows is evident; it is distinct and almost continuous anteriorly, but becomes less distinct posteriorly and is not evident on posterior fourth of body; a series of small black spots placed in the middle of this line at every second or third scale; these spots visible nearly to tail; a somewhat similar series of spots and light streaks, but much less evident, between the seventh and eighth scale rows; no dorsal or typical lateral light stripes (the light stripe described above is not the primary light stripe usually referred

to in *Thamnophis*; it is an accessory marking). Belly and tail light slate, chin cream; near the middle and posterior part of belly a very narrow, broken, longitudinal mid-ventral streak is discernible, but nowhere distinct; no dark marks on subcaudal surface; anal plate cream (not slate).

*Specimens Examined.* In addition to the 63 specimens of the type series, I have examined 16 others, including FMNH No. 1384(6), USNM Nos. 23985-9, Durango, and FMNH No. 1500, Coyotes, *Durango*; USNM Nos. 46411-4, La Parada, *San Luis Potosí*. Records in the literature referable to this race are from Guadalajara, Nevado de Colima, La Laguna and Colonia Brizuela, *Jalisco*; Tupátaro and Guanajuato, *Guanajuato*; and Tangancicuaro, *Michoacán*.

*Variation.* In 59 specimens, 13 have the second labial in contact with the nasal on

### Scale Counts in *melanogaster canescens* (Females).

Museum	Number	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptcc.
FMNH	1384	19-19-17	145	63	8-8	10-10	1-1	3-3
"	1384	"	146	61	8-8	10-10	2-2	3-3
"	1384	"	138	53	8-8	10-10	2-2	2-2
"	1384	"	143	55	9-9	10-10	2-2	2-2
"	1529	"	145	57	8-8	10-10	1-1	2-2
"	1529	"	143	57	8-8	10-10	2-2	2-2
EHT-HMS	†4925	"	142	59	8-8	10-10	2-2	2-2
"	†4928A	"	141	59	8-8	10-10	2-2	2-3
"	†4929	"	140	60	8-8	10-10	2-2	3-3
"	†4930	"	145	55	8-8	10-10	2-2	2-3
"	†4932	"	142	56	8-8	10-10	2-2	2-2
"	4969	"	145	57	8-8	10-10	2-2	2-2
"	4971	"	143	60	8-8	10-10	2-2	2-2
"	4972	"	145	59	8-8	10-10	2-2	3-3
"	5019	"	137	56	8-8	10-10	2-2	3-3
"	5020	"	142	55	8-8	9-10	2-2	2-2
"	5021	"	146	—	8-8	10-10	2-2	3-3
"	5022	"	138	54	8-8	10-10	2-2	2-2
"	5025	"	139	60	8-8	10-10	2-2	2-2
"	5026	"	144	59	8-8	10-10	2-2	2-3
"	5031	"	138	55	8-8	10-11	2-2	2-2
"	5033	"	145	55	8-8	10-10	1-2	2-3
"	5035	"	139	55	8-8	10-10	1-2	2-2
"	5036	19-19-16	137	55	8-8	9-10	2-2	2-2
"	5037	19-19-17	141	51	8-8	10-10	2-2	2-2
"	5038	"	141	56	8-8	10-10	2-2	2-2
"	5039	"	143	54	8-8	10-10	2-2	2-2
"	5040	"	140	58	8-8	10-10	2-2	2-2
"	5041	19-19-16	147	58	8-8	10-10	1-2	2-3
"	5042	19-19-17	140	—	8-8	10-10	2-2	2-2
"	5043	"	143	55	7-8	10-10	1-2	2-2
"	5064	17-19-17	140	60	8-8	10-10	2-2	2-2
"	5065	19-19-17	141	—	8-8	10-10	2-2	2-2
"	5067	"	147	61	8-8	10-11	2-2	2-3
"	5068	"	147	58	8-8	10-10	2-2	2-2
"	5069	"	143	57	8-8	10-10	2-2	2-2
"	5070	"	146	57	8-8	10-10	2-2	2-3
"	4984A	"	139	—	8-8	9-10	2-2	3-3
"	4984B	"	137	55	8-8	10-10	2-2	3-3
USNM	23988	"	140	52	8-8	10-10	1-2	2-2
"	23989	"	142	55	8-?	11-?	2-?	?-?
"	46411	"	147	—	8-8	10-10	2-3	3-3
"	110799	19-19-16	143	—	8-8	10-10	2-2	2-2
"	110800	19-19-17	145	49	—	—	—	—

† Young of No. 5021



both sides, 12 on one side, 34 on neither side. In 79 specimens, the postoculars are 2-2 in 39, 2-3 in 18, 3-3 in 21, 3-4 in one. The ventrals vary from 143 to 155 in males, average 148.3; in females they are 137 to 147, average 142.3. The caudals are 59 to 73 in males, average 66.4; in females they are 49 to 63, average 56.6. Other details of the variation in scutellation are given on the accompanying table.

The largest specimen examined is a female (No. 5069) measuring 751 mm. in total length, the tail 155 mm. The largest male (No. 4973) measures 622 mm. in total length, the tail 146 mm.

In color there is considerable variation. There are two notable patterns. One, the more common, is exemplified by the holotype. In this type there is no very prominent dorsal pattern; most clearly evident is a lateral series of small spots in the third and fourth scale rows. A female of this type (No. 5038) contained seven young (Nos. 4896, 4921, 4934, 4936, 4939-41), all with the same pattern with the exception of one that is completely melanistic (there is also one completely black adult, No. 5022).

In the second pattern type, the spots in the two rows described in the type are much enlarged, although not with sharply defined or regular edges; the spots do not meet; the belly may have irregularly-placed spots near the midventral line, two or three on each ventral scale. One female (No. 5021) of this type contained eleven young, and all are marked dorsally like the mother, with very prominent spots; some have scattered dark spots on the belly, others have a midventral line or no marks whatever.

The constancy of pattern in the young suggests that there may be more than one form involved. There are five adults (Nos. 4969, 4973, 5021, 5030-31) that definitely belong to the distinctly-spotted group, 35 that belong to the nearly unicolor group, and one that is more or less intermediate

(No. 5034). Since the spotted specimens form such a small proportion of the adult population, it might be expected that, if the variant were of a normal type, there would be an equally small proportion of the young with such a pattern. That all the young of one female is the same, the rarer, type is distinctly unusual.

In no specimen is a middorsal light stripe present. Some show slight evidence of a lateral light stripe anteriorly, on the second and third scale rows.

*Remarks.* There seems to be little doubt of the distinctness of the two races of *melanogaster*. In greater doubt is the allocation of the names, and the identity of the spotted specimens from Chapala. The western race, *m. canescens*, ranges from eastern Guanajuato and Michoacán and southern San Luis Potosí westward to the Nevado de Colima and central Nayarit, northward to central Durango. It is possible that the Durango specimens may be distinguishable from the others, for 3-3 postoculars and 1-1 or 1-2 preoculars frequently occur in them. Specimens from that area have not been re-examined during the study of this species and are thus not included as paratypes. The Tepic specimens are typical, non-spotted. The Celaya specimens show some evidence of approach to *m. melanogaster*, as the midventral stripe is somewhat broader than in others of *m. canescens*.

### *Thamnophis rufipunctatus* (Cope).

The type of *angustirostris* (No. 959) has the appearance of a hybrid between *melanogaster* and the species which has been known since 1908 (Ruthven. op.cit., pp. 120-124) as *angustirostris* (= *rufipunctatus*). That it cannot be identified with the species long known by that name has already been noted by Taylor (Taylor & Knobloch, *Proc. Biol. Soc. Wash.*, vol. 53, pp. 129-130, 1940). The essential differences between these two species may be contrasted as follows:

	<i>rufipunctatus</i>	<i>melanogaster</i>
Dorsal pattern	Upper row of spots distinct	No upper row of spots, lower row poorly defined
Ventral pattern	Irregularly mottled	Nearly all black, or a midventral dark line
Head pattern (juv.)	Labia strongly barred, head mottled	Labia indistinctly barred, head not mottled
Preocular	Never one	Occasionally one
Labials enter eye		Two
Dorsal scales	One	19-19(17)-17
Ventrals	21-21(23)-17	♀ 137-153 (69 counts)
Caudals	♀ 152-160 (9 counts)	♀ 49-63 (60 counts)
Range	♀ 65-68 (5 counts)	San Luis Potosí
	Durango to Arizona	Mexico City to Durango and



The type of *angustirostris* has a very distinct body pattern, with well defined spots in the upper row as well as the lower; the labia are somewhat more strongly barred than in typical *melanogaster*; and the dorsal scales are in 21-21-17 rows. In these characters it is more nearly like *rufipunctatus*. It also has a nearly completely black belly, head nearly uniform except labial marks, one preocular, two labials entering orbit, and 149 ventrals. In these characters it is like *melanogaster*. In caudal count the type is exactly intermediate between the two species, having 64 (female). Since the type is from a locality intermediate between the known ranges of *melanogaster* and *rufipunctatus* there can be little question that it may be considered a hybrid.<sup>5</sup> It may be an intergrade (i.e., of a fertile hybrid population), but the fact that both *rufipunctatus* and *melanogaster* are distinguishable in one locality (Coyotes, Durango, FMNH) indicates that the hybrids, if and when produced, are not fertile. Accordingly *angustirostris* gives no evidence in support of a view that *rufipunctatus* and *melanogaster* are subspecies.

The proper name for the northern form is open to question. In general the procedure is to let stand for hybrids those names based upon them, and accordingly *angusti-*

*rostris* cannot be applied to either of the parent species. The next earliest name available is *rufipunctatus*, which also unfortunately is based upon an atypical (partial albino?) juvenile. The type (No. 8600) now lacks all dorsal markings although Cope described it with red spots. In belly pattern it is typical. The head pattern cannot be discerned. The scutellation is typical, with the exception that two labials enter the orbit (a rare occurrence, but seen in other specimens). There are 173 ventrals; 86 caudals (♂); 8-9 supralabials; and 21-21-17 scale rows. It is not an anomalous *Natrix valida*, which has 139 to 154 ventrals (Van Denburgh, 1922). A later name, *Atomarchus multimaculatus* Cope, is without question referable to this species (cf. Taylor & Knobloch, loc. cit.)

Twenty-six Mexican specimens examined are from the following localities. *Chihuahua*: Colonia Juárez (FMNH No. 1096); Ahumada (FMNH No. 1259); San Andrés (FMNH No. 1275a); Chihuahua (Nos. 14254, 14261, 14265, 14271, 14275, 14286, 14288); Río Casas Grandes (No. 2659); Meadow Valley (No. 26592); Arroyo del Alamos, 70-74 kilometers south of Nueva Casas Grandes (Nos. 42874-5); Guadalupe y Calvo (No. 46368); Río Papagochic, Guerrero (No. 95607); Progreso (Nos. 104658-61), Mojárachic (EHT-HMS No. 23015). *Durango*: Coyotes (FMNH No. 1501-2); Guanacevi (No. 46369). *Sonora*? (No. 21055).

<sup>5</sup> The possibility that it represents a distinct species still remains, however; only further specimens from the area represented by the type will show conclusively which interpretation is correct.

Scale Counts in *rufipunctatus*.

Museum	Number	Sex	Scale Rows	Ventrals	Caudals	Supral.	Infral.	Proc.	Ptoc.	Enter Labials Eye
EHT-HMS	23015	♀	21-21-17	156	64+	9-9	12-12	3-3	3-4	1
FMNH	1259	♀	21-21-17	158	—	8-8	10-11	3-3	3-4	1
USNM	14275	♀	21-21-17	152	68	8-9	10-11	3-3	3-4	1
"	14288	♀	21-21-17	160	67	9-9	10-11	3-3	3-4	1
"	26591	♀	21-21-17	155	—	8-8	10-10	2-2	3-3	1
"	26592	♀	21-23-17	160	65	8-9	10-11	3-3	4-4	1
"	104658	♀	21-21-17	154	—	8-9	10-11	2-3	2-?	1
"	104659	♀	21-21-17	158	—	8-8	10-10	2-2	3-3	1
FMNH	1501	♀	21-21-17	156	68	8-8	10-10	2-2	3-3	2
"	1096	♂	21-21-17	162	79	8-9	10-10	2-2	4-4	1
"	1275a	♂	21-23-17	163	78	8-8	9-9	3-3	3-4	1
USNM	14254	♂	21-21-17	161	—	8-8	10-10	2-3	2-3	1
"	14261	♂	21-21-17	162	76	8-?	10-?	2-3	3-3	1
"	14261	♂	19-21-17	158	—	8-8	10-10	3-3	3-4	1
"	14265	♂	21-21-17	160	79	8-8	10-10	2-2	3-3	1
"	14271	♂	21-21-17	164	80	8-?	11-?	3-3	3-4	1
"	14286	♂	19-21-17	159	82	8-9	11-11	3-3	3-4	1
"	42874	♂	21-21-17	163	—	8-8	10-10	2-2	3-4	1
"	42875	♂	21-21-17	165	—	7-8	10-10	2-2	3-3	1
"	46368	♂	21-21-17	174	76	8-8	10-10	2-3	3-3	1
"	46369	♂	21-21-17	177	78	8-9	9-10	2-3	3-4	1
"	95607	♂	21-21-17	166	77	8-8	10-10	2-3	3-3	1
"	104660	♂	21-21-17	159	—	8-8	10-11	2-2	3-3	1
"	104661	♂	21-21-17	162	76	8-8	9-10	2-4	2-4	1
FMNH	1502	♂	21-21-17	165	—	8-8	10-11	2-2	3-3	1
USNM	21055	♂	21-21-17	164	79	8-8	10-10	2-2	3-3	1

KEY TO MAINLAND MEXICAN AND CENTRAL AMERICAN *Thamnophis*.

1. Lateral stripe involving third and fourth scale rows on anterior part of body...2  
Lateral stripe not involving fourth row, indistinct, absent, or involving only the second or third row or both.....5
2. Scale rows 21 at middle or on anterior third of body; anterior edges of ventrals black.....3  
Scale rows 19, maximum (except immediately behind head).....4
3. Caudals 78 or less in males, 68 or less in females...*macrostemma macrostemma*  
Caudals 79 or more in males, 69 or more in females.....*macrostemma megalops*
4. Caudals 93 to 104, ventrals 155 to 169, totals 255 to 262 in females; 102 to 109, 158 to 172, and 260 to 277, respectively, in males.....*sauritus proximus*  
Caudals 83 to 96, ventrals 142 to 159, totals 229 to 254 in females; 92 to 99, 149 to 158, 245 to 256, respectively, in males.....*sauritus chalcus*
5. Scale rows 21 or more on anterior third of body.....6  
Scale rows less than 21.....10
6. Preoculars two or more; usually one labial entering orbit.....*rufipunctatus*  
Preocular single; usually two labials entering orbit.....7
7. Usually anterior edges of ventrals black, and the entire belly clouded, but never a longitudinal dark line or entire belly black; chin and sometimes subcaudal surface cream, sharply differentiated from dark belly color.....3  
Not so; belly unmarked or with a longitudinal dark line, or nearly entirely black, or with scattered dark spots; chin and subcaudal surfaces not sharply differentiated from dark color of belly...8
8. Belly almost completely black (or perhaps a midventral black stripe); lateral light stripe not restricted to third row anteriorly.....*angustirostris*  
Belly not with a median, more or less extensive black stripe; lateral stripe, when evident, restricted to third row anteriorly.....9
9. Vertebral light stripe one and two half scale rows wide, at least at base of tail.....*marcianus*  
Vertebral light stripe one scale row wide, or nearly indistinguishable, even at base of tail.....*ruthveni*
10. Preoculars two or more, rarely one; belly usually with a continuous, longitudinal black area on center; scale rows 19 on anterior third of body.....11  
Preoculars single; belly not with a continuous black area (or if so, scale rows no more than 17).....12
11. Black on belly and tail very extensive, covering nearly all of ventral surface; vertebral and lateral light stripes evident in all except large specimens; second labial generally (81%) in contact with rostral; postoculars usually (75%) 3-3 or more; caudals usually 64 or less (84%) in males, 54 or less (73%) in females...*melanogaster melanogaster*  
Black on belly and tail entirely absent or restricted to a midventral line or a few scattered spots; rarely light lines evident, never the middorsal; second labial usually not (78%) in contact with rostral; postoculars usually (72%) 2-2 or 2-3; caudals usually over 64 (69%) in males, 55 (84%) in females  
*melanogaster canescens*
12. Maximum dorsal scale rows 17, and no evidence whatever of a middorsal stripe on any part of body...*chrysocephalus*  
Dorsal scale rows more than 17, or if only 17, a vertebral light stripe present or indicated on some part of body.....13
13. A moderately dark area in middle of each parietal, sometimes fused with nuchal blotches, darker than most of the remainder of the dorsal surface of head (light).....14  
No distinct dark mark on center of parietal; head nearly uniform light or dark above.....15
14. Large spots present on body, usually a single series extending completely across back.....*phenax phenax*  
Spots on body (except on neck) poorly defined or absent...*phenax halophilus*
15. The spots in the two rows on each side, between the vertebral and lateral stripes, fused together over most of body (not just on neck).....17  
The spots in the two rows on each side, between the vertebral and lateral stripes, not fused together except on neck; spots disappearing posteriorly or not.....16
16. Scale rows anteriorly 17<sup>6</sup>.....17  
Scale rows anteriorly 19.....19
17. Dark color of dorsal surface of head and nape with a clearly defined, dark-edged indentation a little posterior to angle of mouth, extending anterodorsally toward midoccipital region; scale rows usually 19 on some part of body; spots usually distinct on most of body.....18  
Dark color of dorsal surface of head and nape lacking any clearly defined, dark-edged light indentation behind angle of mouth; scale rows seldom over 17 on any part of body; no spots distinct on body posterior to nape, dorsum nearly uniform brown.....*scalaris godmani*
18. Scale rows posteriorly usually 17 (94%); anterior scale rows usually 19 (88%)  
*scalaris scalaris*  
Posterior scale rows usually less than 17 (70%); anterior scale rows usually less than 19 (93%).....*scalaris scalaris*
19. Spots in upper row of the two series between vertebral and lateral light lines fused together and usually with the spots in the outer row, the latter spots remaining distinct from each other; ground color red between spots of outer row (above lateral stripe); middorsal stripe well-defined...*sirtalis parietalis*  
Spots not fused in such a manner, although sometimes poorly defined or corresponding spots of the two rows fused together; ground color not red; middorsal stripe distinct or not.....20

<sup>6</sup> Some care must be used to determine whether the scale rows are reduced to 17 at any point on the anterior part of body.

20. Middorsal stripe with continuous, straight edges, covering one and two half scale rows; rounded dark spots on anterior edges of ventrals on sides of at least part of belly; ventrals seldom over 157, caudals seldom over 76.....21

Middorsal stripe usually covering only the vertebral row, or indistinct, or absent; if broader, not straight edged and ventrals and caudals more numerous; belly not spotted .....22

21. Supralabials strongly barred; head dark above, the color fused with that of nape; ventrals 136 to 140

*sumichrasti praeocularis*

Supralabials not or weakly barred; head light above, its color sharply differentiated from that of nape; ventrals 144 to 167 .....*sumichrasti cerebrosus*

22. No median light stripe on any part of body, its place occupied by a median series of dark spots.....27

A median light stripe at least anteriorly; no median series of dark spots.....23

23. A very distinct median light stripe throughout length of body; and dark spots present on the scales below the lateral light line at least anteriorly, visible without spreading the scales; ventrals seldom less than 149.....24

Median light stripe indistinct or absent posteriorly; or, if distinct posteriorly, no dark spots on the scales below the lateral light line .....25

24. Ventrals 167 or more in males, 163 or more in females.....*eques cyrtopsis*

Ventrals 166 or less in males, 162 or less in females.....*eques eques*

25. Ventrals 155 to 166....*ordinoides errans*

Ventrals fewer, 136 to 153.....26

26. Median light stripe scarcely distinguishable on any part of body, and nowhere more than one scale row wide

*eques postremus*

Median light stripe covering one and one half to three scale rows anteriorly, but disappearing completely on posterior part of body.....*sumichrasti fulvus*

27. Ventrals 139 to 157 in males, in females 139 to 147; caudals 58 to 72

*sumichrasti sumichrasti*

Ventrals 155 to 162 in males, 149 to 156 in females; caudals 78 to 89....*vicinus*



## 18.

Membracidae (Homoptera) from British Guiana.<sup>1</sup>

W. D. FUNKHOUSER

University of Kentucky.

[This is one of a series of papers dealing with the collections made at Kartabo, British Guiana, at the Field Station of the Department of Tropical Research of the New York Zoological Society, under the direction of Dr. William Beebe. During the eight years of the maintenance of the station, extensive collections and ecological studies were made within an area of jungle one-quarter of a mile square, which may be called the Guiana Jungle-zone. For details concerning this area of intensive study, see *Zoologica*, Vol. VI, No. 1, 1925.]

Miss Maud D. Haviland reported on the first collection of Membracidae from Kartabo in *Zoologica*, Vol. VI, No. 3, 1925. The present paper is the result of Dr. W. D. Funkhouser's study of a second collection.]

## INTRODUCTION.

Through the courtesy of Dr. William Beebe, the writer has had the privilege of examining a very interesting lot of Membracidae collected chiefly in British Guiana. In fact, Dr. Beebe states that practically all of the specimens were taken within a quarter of a square mile of jungle at Kartabo. This small area must certainly have a rich insect fauna since it has yielded nearly fifty different species of one small family.

The collection is particularly valuable, however, in its contribution to our knowledge of the geographical distribution of the Membracidae since a very large number of the listed species represent new locality records. Included in the collection are two species taken at Guanoco, Venezuela, and one in Trinidad.

The species represented in the collection are here reported as follows:

1. *Membracis fusca* DeGeer.

DeGeer, Ins., Vol. III: p. 208, No. 10, Tab. 32, fig. 14. (1773).

Eight specimens from Kartabo and six from Bartica. A large foliaceous bizarre form, originally described from Peru but is

common throughout South America. It has been previously reported from Kartabo by Miss Maud Haviland (Mrs. H. H. Brindley) in 1925.

2. *Membracis foliata* Linn. var. *c-album* Fairm.

Linnaeus, Syst. Nat., Vol. II: p. 705, No. 2. (1767).

Fairmaire, *Revue Memb.*, p. 244, No. 4. (1846).

Ten specimens from Kartabo. Another of the well known foliaceous forms with a wide distribution in South and Central America, its known range extending from Brazil across the northern part of South America and through Central America to Mexico. Fairmaire described the variety *c-album* from British Guiana.

3. *Membracis provittata* Buckt.

Buckton, Mon. Memb., p. 42, Pl. 3, figs. 6, 6a. (1903).

Twenty-two specimens from Kartabo and one from Bartica. This species has been considered a synonym of *tectigera* but is now known to be distinct. Buckton described it from Surinam and we have a long series in our collection from British Guiana. These are the only known localities, for the species is apparently rare and is seldom seen in collections.

4. *Membracis fasciata* Fabr.

Fabricius, Syst. Ent., Vol. II: p. 2092, No. 54. (1767).

One specimen from Kartabo. A striking species very common in Brazil and with a rather confused taxonomic history since it has been redescribed under a large number of synonyms. Miss Haviland reported it from British Guiana in 1925.

5. *Membracis arcuata* DeGeer.

DeGeer, Ins., Vol. III: p. 206, No. 9, Tab. 32, fig. 10. (1773).

One specimen from Kartabo. Common throughout South and Central America and previously reported from British Guiana by Miss Haviland.

<sup>1</sup> Contribution No. 637, Department of Tropical Research, New York Zoological Society.

6. *Enchenopa lanceolata* Stoll.

Stoll, Cic., Tab. 27, fig. 166. (1780).

Four specimens from Kartabo and ten from Bartica. One of the commonest of the neotropical membracids. Reported from all of the northern countries of South America and across Panama into Central America. Previously reported from British Guiana by Miss Haviland.

7. *Enchenopa serratipes* Buckt.

Buckton, Mon. Memb., p. 49, Pl. 5, fig. 9. (1903).

Two specimens from Kartabo. This species has often been confused with *E. albidorsa* Fairm., but is distinct. *E. albidorsa* is abundant throughout South America but we have undoubted records of *serratipes* only from Brazil, British Guiana and Colombia. Miss Haviland reported this species as *albidorsa* from Kartabo.

8. *Campylenchia hastata* Fabr.

Fabricius, Mant. Ins., Vol. II: p. 263, No. 9. (1787).

Two specimens from Kartabo. A widely distributed species, showing some variation in size and color in different regions but found in one phase or another in most parts of South America, Central America and Mexico. One of the common forms of this species was described as *nutans* and was so reported from British Guiana by Miss Haviland.

9. *Leioscyta rufidorsa* Godg.

Goding, Journ. N. Y. Ent. Soc., Vol. XXXVI: p. 37. (1928).

Two species from Kartabo. Goding described this species from Ecuador and it has not been reported in the literature from any other country but we have specimens in our collection from Peru, Colombia and Brazil. This is the first record from British Guiana.

10. *Erechtia punctipes* Buckt.

Buckton, Mon. Memb., p. 53, Pl. 7, figs. 5-5b. (1903).

One specimen from Kartabo. This is apparently a very rare insect and is seldom seen in collections. Buckton gave only "South America" as the locality and it was a long time before it was finally recognized. Finally Goding identified it from Brazil and the writer secured a good series from Peru. This British Guiana specimen gives us a new locality record.

11. *Erechtia brunneidorsata* Funkh.

Funkhouser, Can. Ent., Vol. XLVI: p. 357, Pl. 24, fig. 1. (1914).

Three specimens from Kartabo; one from Bartica. Previously known only from Peru but the British Guiana specimens agree entirely with the type material. A new locality record.

12. *Pterygia uropigii* Buckt.

Buckton, Mon. Memb., p. 72, Pl. 12, fig. 3. (1903).

One specimen from Kartabo. A bizarre form described from Brazil and reported from British Guiana by Miss Haviland in 1925. The writer has a few specimens from Peru. These are the only locality records known.

13. *Pterygia cerviceps* Fowl.

Fowler, B. C. A., p. 24, No. 3, Tab. 2, figs. 12, 12a. (1894).

Two specimens from Kartabo. The center of distribution of this species is certainly Central America where it is quite common but we have seen specimens from Colombia and from Venezuela so it apparently ranges down into South America. This is the first record from British Guiana.

14. *Umbonia spinosa* Fabr.

Fabricius, Syst. Ent., p. 675, No. 4. (1775).

Eighteen specimens from Kartabo. One of the largest, commonest, most widely distributed and most easily recognized of the neotropical Membracidae. Reported from almost every country in South America and Central America. Previously reported from Kartabo by Miss Haviland.

15. *Aconophora marginata* Walk.

Walker, List. Hom. B. M., p. 540, No. 16. (1851).

Eleven specimens from Kartabo. This species is common in Mexico and Central America and has been reported from Panama, Brazil, Ecuador, Peru and Bolivia but this is the first record from British Guiana.

16. *Aconophora pallescens* Stal.

Stal, Hem. Fabr., Vol. II: p. 35, No. 12. (1869).

Two specimens from Kartabo. Another widely distributed species, closely related to the preceding, and reported from the same general regions but never before recorded from British Guiana.

17. *Aconophora fusiformis* Fowl.

Fowler, B. C. A., p. 69, No. 19, Tab. 5, figs. 18, 18a, 19. (1895).

One specimen from Kartabo. This is another Central American form which is only rarely reported from South America. The writer has material from Brazil and Bolivia but the Kartabo specimen gives us the first record from British Guiana.

18. *Aconophora projecta* Funkh.

Funkhouser, Journ. N. Y. Ent. Soc., Vol. XXV: No. 2, p. 160. (1927).

One specimen from Kartabo. Since this species has been recorded from Ecuador, Bolivia, Colombia and Brazil, it would be expected to occur in British Guiana but has

not been previously reported from that country. Another new locality record.

19. *Darnis partita* Walk.

Walker, *Ins. Saund.*, p. 75. (1858).

Five specimens from Kartabo and one from Bartica. When Miss Haviland reported this species from Kartabo in 1925 it was the first record from South America but since then we have secured specimens from Peru, Ecuador, Panama, Canal Zone and Colombia. It would therefore seem that its range extends along the northern coast of South America.

20. *Darnis latior* Fowl.

Fowler, B. C. A., p. 52, No. 2, Tab. 4, figs. 16, 16a. (1894).

One specimen from Kartabo. This is another new locality record but the species has been found in Peru, Ecuador and Colombia so its distribution is probably about the same as that of *partita*.

21. *Stictopelta fraterna* Butler.

Butler, *Cist. Ent.*, Vol. II: p. 340, No. 9. (1878).

One specimen from Kartabo and one from West Bank. Again a new locality record. It was described from Peru and both Goding and Fowler reported it from Mexico. We have specimens in our collection from Colombia and Bolivia. These localities with this British Guiana record represent its present known distribution.

22. *Nassunia binotata* Fairm.

Fairmaire, *Revue Memb.*, p. 291, No. 3. (1846).

Three specimens from Kartabo. A very rare species, almost never seen in collections and previously known only from Brazil. A new locality record.

23. *Heteronotus tridens* Burm.

Burmeister, *Rev. Silb.*, Vol. I: p. 229. (1833).

Seven specimens from Kartabo. The largest species of its genus, very grotesque in appearance, strikingly marked and very well known. Common in northern South America but this is the first time it has been reported from British Guiana. Another new locality record.

24. *Heteronotus spinosus* Lap.

Laporte, *Ann. Soc. Ent. France*, Vol. I: p. 96, Pl. 3, fig. 7. (1832).

Four specimens from Kartabo. Closely related to the preceding and showing considerable variation so that it has been described under several synonyms. Its distribution seems to be about the same as that of *H. tridens* of which it may be merely a variety. Miss Haviland reported it from British Guiana under the name *Heniconotus armatus*.

25. *Cymbomorpha dorsata* Fairm.

Fairmaire, *Rev. Memb.*, p. 293, No. 6. (1846).

One specimen from Kartabo and one from Guanoco, Venezuela. Both the British Guiana and the Venezuela records are new. It has previously been reported only from Brazil, Peru and Costa Rica.

26. *Horiola picta* Coq.

Coquebert, *Ill. Ic.*, p. 78, Tab. 18, fig. 10. (1801).

One specimen from Trinidad. The commonest species of its genus, found in most parts of South America, Central America and the West Indies but not previously recorded in the literature from Trinidad so that this also is a new locality record.

27. *Horiola lineolata* Fairm.

Fairmaire, *Rev. Memb.*, p. 492, No. 2. (1846).

Three specimens from Kartabo. Closely related to the preceding species and with about the same range. It is commonly found in Brazil and Colombia but has not been previously reported from British Guiana.

28. *Ceresa sallai* Stal.

Stal, *Hem. Mex.*, p. 70, No. 421. (1864).

A good series of thirty-one specimens from Kartabo. This species was described from Mexico where it is abundant and it is common in Central America. It is reported only rarely from South America, the only known records being from Brazil and Bolivia. This is the first record from British Guiana.

29. *Ceresa vitulus minor* Fowl.

Fowler, B. C. A., p. 103. (1894).

Five specimens from Kartabo. This is the small variety of *C. vitulus* Fabr. which seems to occur with *vitulus* wherever *vitulus* is found. *C. vitulus* was reported from British Guiana by Miss Haviland but this is the first record of the variety from that country. It is found throughout South America.

30. *Micrutalis pallens* Fowl.

Fowler, B. C. A., p. 118, No. 4. (1895).

One specimen from Kartabo. This is a common species in Mexico and Central America but has not been reported in the literature of the family from South America. However we have two specimens in our collection from Venezuela so it is not surprising to see it from British Guiana. This is a new record from British Guiana and the first published record from South America.

31. *Boethoos reticulata* Fabr.

Fabricius, *Syst. Rhyng.*, p. 29. (1803).

Two specimens from Kartabo. Apparently abundant in Brazil, Colombia and Venezuela and previously reported from British Guiana by Miss Haviland.

32. *Vanduzeeia triguttata* Burm.

Burmeister, *Rev. Silb.*, Vol. IV: p. 183, No. 4. (1836).

Two specimens from Kartabo. The dominant species of its genus in southwestern United States, Mexico and Central America. The South American forms which are found in Colombia and Venezuela are slightly different in minor respects from the northern ones but we believe that they are all of the same species. This is the first record from British Guiana.

33. *Stylocentrus ancora* Perty.

Perty, *Del. Anim.*, p. 179, Pl. 35, fig. 15. (1834).

One specimen from Kartabo. Very abundant in Brazil and recorded from Ecuador, Colombia and Venezuela. This is the first record from British Guiana.

34. *Cyphonia clavata* Fabr.

Fabricius, *Mant. Ins.*, Vol. II: p. 264, No. 17. (1878).

Eight specimens from Kartabo and one from West Bank. One of the commonest membracids in South America and found in all of the northern and central areas of that continent. Reported from British Guiana by Miss Haviland in 1925.

35. *Cyphonia proxima* Guer.

Guerin,  *Ic. Reg. Anim. Ins.*, p. 365, Tab. 59, fig. 3. (1838).

Two specimens from Kartabo. A less abundant species than the preceding but with a range extending from Mexico through Central America and Panama to northern South America. This, however, is the first record from British Guiana.

36. *Antianthe expansa* Germ.

Germar, *Rev. Silb.*, Vol. III: p. 245, No. 1. (1835).

Three specimens from Guanoco, Venezuela. One of the best known and most widely distributed of the American Membracidae. It has been reported from practically every country in South and Central America and extends northward into Florida, California and Arizona.

37. *Amastris antica* Germ.

Germar, *Mag. Ent.*, Vol. IV: p. 16. (1821).

Two specimens from Kartabo. A very rare species previously known only from Brazil and Peru. It is quite distinct from all other species of the genus and is easily recognized. A new locality record.

38. *Amastris obtogens* Fabr.

Fabricius, *Syst. Rhyng.*, Vol. II: p. 25. (1803).

Seven specimens from Kartabo. The best known and probably the most abundant of the species of the genus but not previously

reported from British Guiana. The specimens most often seen in collections are from Brazil, Colombia, Ecuador and Peru. A new locality record.

39. *Amastris compacta* Walk.

Walker, *List Hom. B. M. Suppl.*, p. 140. (1858).

Two specimens on one pin from Kartabo. A well known and rather widely distributed species, fairly common in Brazil, Peru, Ecuador and Colombia but this is the first record from British Guiana.

40. *Amastris minuta* Funkh.

Funkhouser, *Journ. N. Y. Ent. Soc.*, Vol. XXX: No. 1, p. 30, fig. 6. (1922).

One specimen from Kartabo. This species has never been mentioned in the literature of the family since its original description and so far as we know this is the second specimen ever to be found since the type was a single specimen from Peru. Of course this is a new locality record.

41. *Hille exaltata* Walk.

Walker, *List Hom. B. M. Suppl.*, p. 140. (1858).

Two specimens from Kartabo. This species has been reported in the literature only from Brazil but we have specimens in our collection from Peru and Colombia. This is the first record from British Guiana.

42. *Hille herbicola* Hav.

Haviland, *Zoologica*, Vol. VI: No. 3, p. 255, Pl. 4, figs. 1, 1a. (1925).

Three specimens from Kartabo. This species was described from Kartabo and has never been reported from any other locality.

43. *Tynelia hirsuta* Funkh.

Funkhouser, *Journ. N. Y. Ent. Soc.*, Vol. XXX: No. 1, p. 25, Pl. 3, fig. 1. (1922).

One specimen from Kartabo. Described from Peru and we have seen material from Nicaragua. This is the first record from British Guiana.

44. *Rhexia pallescens* Fabr.

Fabricius, *Syst. Rhyng.*, Vol. II: p. 28, No. 8. (1803).

One specimen from Kartabo. A species which has been described under a number of different specific names in at least five different genera. It is quite common throughout northern South America and shows considerable variation in color. It seems to be most abundant in Brazil, Surinam, Colombia and Ecuador. This is a new record from British Guiana.

45. *Stegaspis insignis* Buckt.

Buckton, *Mon. Memb.*, p. 59, figs. 6, 6a. (1903).

Three specimens from Kartabo. One of the peculiar "dried leaf" forms which al-



ways attract attention and are often seen in collections. Most of the material which we have seen has been from Brazil, Peru, Ecuador and Colombia. This is the first record for British Guiana.

46. *Stegaspis laevipennis* Fairm.

Fairmaire, *Rev. Memb.*, p. 527, No. 14. (1846).

Four specimens from Kartabo. Another of the brown, foliaceous species of this genus with about the same distribution as the preceding. It was reported from British Guiana by Miss Haviland in 1925.

47. *Lycoderes hippocampus* Fabr.

Fabricius, *Syst. Rhyng.*, p. 20, No. 22. (1803).

One specimen from Kartabo. Apparently a very rare species. It was reported from British Guiana in 1925 by Miss Haviland but was known previously only from Brazil

and has never been recorded from any other countries.

48. *Bocydium globulare* Fabr.

Fabricius, *Syst. Rhyng.*, p. 16, No. 3. (1803).

Two specimens from Kartabo. A species often figured to illustrate a most bizarre type of pronotal development, especially because of the globules on the bar above the head. However it is not common. It was described from Brazil and we have specimens from Peru. It has not been previously recorded from British Guiana.

49. *Tolania opponens* Walk.

Walker, *List Hom. B. M. Suppl.*, p. 159. (1858).

Three specimens from Guanoco, Venezuela. One of the few membracids which completely lack a posterior process. Very abundant throughout South America, Central America and Mexico.



## 19.

## A Consideration of Evolutionary Hypotheses in Reference to the Origin of Life.

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(Text-figure 1).

### INTRODUCTION.

The living organisms of today are thought by most biologists to have evolved from more or less dissimilar ancestors. In fact, since the time of Charles Darwin biologists have addressed themselves, in the main, to establishing evidence to support or demolish various propositions concerning the mode of evolution, as set up by him or others who followed him to a greater or lesser extent. It seems not to have occurred to many such students that the importance to be attached to interpretations of the results of their studies must vary with our ideas concerning the origin of life. Since we are in no position to make any postulates, it may be useful to consider the various ideas that have arisen from time to time in reference to their bearing on the acceptability of any particular evolutionary hypothesis.

We may go along with Lotka (1925) in his policy of resignation concerning a definition of life without in any way encountering difficulty in an attempt to discuss the possibilities of origin. Many of the attempts to explain the origin of life have come from non-scientific groups and most of these may be dismissed with a few words. All are included in this discussion since their many interlocking ideas make it essential at least to mention each one.

The author is grateful to Dr. Richard T. Cox of New York University for checking the physical parts of the discussion, to Prof. Albert E. Parr of the American Museum of Natural History, for helpful criticism, to Dr. G. E. Hutchinson of Yale University, for valuable suggestions, and to Mr. J. W. Atz for editorial assistance.

### CONCEPTS OF THE ORIGIN OF LIFE.

Although superficially numerous, see Woodruff (1936), all the ideas that have been put forth concerning the possible origin of life are reducible to two basic patterns. These may be discussed separately

for the purpose of considering their tenable contents in reference to the adequate interpretation of evolutionary experiments and arguments.

1. *Planted life forms.* The idea that life may have been planted on the earth from some exterior source has always been attractive, but today it seems less reasonable than ever before. The idea divides into two parts.

a. *Normal cosmic behavior.* One idea has been that simple, very resistant particles drifting through space from other planets or similar bodies may revive to an active life when happening to land on a body of suitable environment. Arrhenius (1908, 1911) by ingenious reasoning even went so far as to suggest that thermophilic bacteria rained on the earth from possibly Venus, being impelled by the radiant energy of the Sun. This is mentioned in this connection merely to indicate that such possibilities have been given consideration by thoroughly serious persons. Certainly modern experiments on the effects of low pressure and temperatures have shown nothing tending to make this an impossibility as has been indicated, for instance, by Goertz (1928). Venus itself as a source of living substance would seem unlikely on the basis of the view of Wildt (1940) who argues for a negligible amount of water and an atmosphere of formaldehyde. See also Jeans (1942). Such a condition would not seem likely as a life source, in spite of the fact that certain molds and dipterous larvae appear to thrive on relatively low concentrations of formaldehyde in aqueous solution. Since Venus evidently rotates, although its speed has not been determined, it would appear that its nearness to the Sun, surface temperatures as high as 60°C having been recorded, would also stand in the way of the continued existence of protoplasm at any place on its surface. The effects of unfiltered solar or other radi-

ation in space, moreover, may represent a very real hazard. Oparin (1938) on this basis presents a very convincing argument against the possibility of survival under such radiation.

In effect, this idea would have interstellar space occupied by viable motes passing from place to place, along with the matter and radiations already known to be there. Such a condition would provide for a polyphyletic origin of terrestrial life, if evolutionary capabilities be ascribed to such organisms. Lipman (1932) thought he had succeeded in reviving bacteria from the interior of stony meteorites. Oparin (1938) dismisses this study by expression of the belief that contamination was responsible. Actually, while such may have been the case, Oparin gives no foundation for so assuming, other than his well-reasoned argument against organisms surviving the radiations of interstellar space. He wrote, "The organisms which he [Lipman] succeeded in isolating were identical with the bacterial forms existing on the Earth. This makes it very probable that, in spite of all his precautions, Lipman did not succeed in preventing earth bacteria from contaminating the meteorites while they were ground to a powder. Even in different regions of our planet there are different forms of microorganisms, and it would be extremely strange if exactly the same bacterial forms found on the Earth were present also on some remote planets." Exception is taken to this last remark, for if Lipman is right, such results, on the contrary, are exactly what one should expect. Since meteorites are continually falling to earth, one then should also expect a continual seeding of forms capable of surviving such transit. These then would be expected to be common on the Earth in proportion to its ability to support them in active life. This, indeed, also might well lead to a spotty distribution dependent on their needs. Beutner (1938b) also rejects such a possibility but submits no further closely reasoned arguments. Jones (1940) treats the subject in a similar fashion.

**b. Special events.** The planting of organisms on earth, on the other hand, may be thought of as a special event, more or less unique in cosmic history. Anything that could be conjured up to induce such an event would be classified here. The creation of life by decree would come here and would be practically the equivalent of the planting of a culture by some space-traveling, superior animal. Space travel is one of the most recent serious aspirations of man and as yet is seriously handicapped, to say the least, on technological grounds. If extra-terrestrial beings have developed such an art, we certainly have no evidence of it, but the fact that there have been no

visits to earth establishes nothing. It might even be imagined that life on earth is the remnant of some ill-fated expedition from another body from which only food animals survived. The possibilities of this sort are limited only by one's imagination and have been well covered by the writers of scientific fiction, and need not longer detain us here.

Other special events in the nature of a cosmic accident happening but once could make a single planting. Such an accident would provide for a monophyletic origin or a polyphyletic one to the extent of the variety of organisms in this single seeding. One thinks of the cluster of asteroides between Mars and Jupiter that supposedly represents a disrupted planet of considerable size. Its disintegration must have scattered material far and wide.

Fantastic as these notions may sound, there is but one other basic pattern of source that has been suggested which, as will be seen later, also has its fantastic side. The idea that living entities were created by fiat is a widespread one among theologists' mysticisms, which, with minor variations, is the common property of many theologies. Such ideas could belong in the category of special events, if not mere figments of wishful thinking.

**2. Spontaneous generation.** The long-discredited belief in spontaneous generation, experimentally unsupported, is nevertheless the idea which most scientific men seem to think best accounts for the origin of life. By the simple expedient of pushing the event far enough back into geologic time to prevent any kind of experimental approach and postulating an unknown but suitable environment, many seem to have eased their minds. This interpretation of life origin likewise divides into two parts parallel to those of item number one.

**a. Chemical evolution.** Given a sphere such as the Earth, chemists, physicists, astronomers and geologists have shown that a chain of events must follow due to the interaction of forces involved. Radioactive degradation, the salt concentration of the ocean, and so on, come to mind, which it is unnecessary to discuss at length here. See, for example, Clarke (1924), Fairchild (1938) and Jones (1940). The point of this is that chemical evolution proceeds systematically according to the second law of thermodynamics and is very definitely identifiable as a kind of inorganic orthogenesis. Thus we have a world stage in which the inorganic props and scenery are changing by an orthogenetic or "built in" process. Oparin (1938) devotes nearly an entire book to visualizing how such chemical changes took place. He gives by far the most careful analysis and the most plausible picture of a cooling

Earth. Whether all his details are sound and whether events lead automatically to living entities or not, it is hard to deny the basic soundness of his chemical evolution. Beutner (1938) arrives at a very similar conclusion, differing chiefly in the order of chemical events but lacking the close reasoning of Oparin. Riddle (1939) sketches his similar views with extreme brevity. Jones (1940) gives a presentation of the theoretical and observational data of astronomy, indicating what is known and fairly inferential of the conditions on other planets in reference to the basic needs of life.

If the idea is valid that in this process there automatically comes a time and a concatenation of events which grade from the strictly inorganic to the organic and the sentient, then we have life beginning as of necessity as a part of a general "orthogenesis." As such an event would hardly occur simultaneously throughout the world, presumably there would be started various orthogenetic series, the first advanced in development as compared with the later. This should go on until the period of its possibility is passed by the general orthogenesis of the whole system, repetition becoming impossible when the stage is sufficiently changed. This point would be passed presumably when there were no longer any large sterile areas. Oparin believes that early sterility is *absolutely essential* for a life origin of this sort. The pre-living organic components would simply be broken down on earth today, long before they reached anywhere near the living state, by the activities of living beings, according to his views.

Lichtig (1938), on the other hand, disregards this point and supposes the transition from lifeless to living matter to be taking place more or less continuously, indicating a widespread polyphylogenesis.

Herrera (1942) proposes an interesting and startling theory which would derive life from the sublimation of volcanic emanations, after years of close study of the life-resembling behavior and physical appearances of a tremendous number of chemical substances. As he indicates, this, too, would imply a continual synthesis of life, unless some peculiar but necessary factor was present but once in the Earth's history.

**b. Rare accident.** If, on the other hand, we do not consider the origin of life as definitely part of the general increasing entropy, then we may consider it as an "accidental" event repeatable as often as the needful circumstances repeat. This, of course, is pure, spontaneous generation in the simple sense, and no doubt, when referred to known physical law, apparently leads such students as Smith (1932) to refer somewhat poetically to life as "an eddy

in the second law of thermodynamics." See Pike (1939) for a recent discussion of various views on the subject.

Both these views may lead to polyphyletism, the first definitely orthogenetic and the second not necessarily so by virtue of questioning the full and simple operation of the second law in living systems.

If, as thought by various students, the origin of life occurred by unique "accident" another element is intruded. This view arose and gained force by the failure of Pasteur *et al.* to produce life by simple means, and the large evidence that life, as we know it, is produced only by pre-existing parents. The rare accident view is perilously close to the fiat creation of theologians, differing largely in use of words, especially since it is doubtful if any sect ever believed that the creation of human beings was an "accident."

This rare accident view should make for a monophyletic origin of life and leave the way open for any evolutionary process whatever. Judging from the literature of evolution, it would seem that most workers in that field imply that they are interpreting their results on the assumption of an origin of this sort. Either the rare accident or the straight chemical evolution could lead at first, at least, only to an orthogenesis. Paired species, parallel specializations, and parallel mutations certainly suggest at least a "charge" of similar potentialities as a recurrent phase in any group of sufficiently numerous organisms. These views are conditioned by whether one considers life as a highly probable or improbable result of the operation of statistical mechanics.

**3. Interaction of methods.** Of these several views, it will seem that evolution could conceivably proceed by any method in all but one. That one, as a part of general chemical evolution, is definitely linked with orthogenesis. All those items in which life would arise by the ordinary working out of natural processes (1a and 2a) would be expected to lead to a polyphyletic condition. A special planting accident (1b) could be either mono- or polyphyletic, while a rare accident of spontaneous generation (2b) would be monophyletic. This interaction is especially pertinent in the case of chemical evolution (2a) and natural seeding from outer space (1a). Since sterility is perhaps necessary for the first, the second presumably could not successfully be brought into play. If extensive seeding did occur early enough, it could, on this basis, check chemical development of the basic organic compounds.

Before proceeding to a consideration of some current biological ideas in reference to the preceding, it may be best to discuss certain theoretical considerations basic to the establishment of life systems.

## NON-PROTOPLASMIC SYSTEMS.

Active life processes as we know them are remarkably limited in their temperature range. It is evident that it must be below the coagulating point of essential proteins (these may range from about 35° to 70°C), and above the freezing point (scarcely below 0°C). Many various forms are able to survive protracted periods far below this, but are in a state of suspended activity until the temperature is raised again. See, for example, Goertz (1938). Warm-blooded animals may, of course, be active below this temperature of environment, but their life processes are going on at a *higher temperature* by virtue of their very pretty trick of operating an internal heating plant.

Since the chief solvent of body fluids is water which exists in the liquid phase only between 100° and 0°, here are essentially the broad limits, 100° never being reached because protein coagulates at a lower point and 0° being slightly passed on the down side because of the lowered freezing point of the mildly saline body fluids.

These remarks, naturally, refer to surface pressures. Actually many aquatic organisms exist at much greater pressures, as, for example, the abyssal fish of great depths with pressures of tons per square inch. Here temperatures may be such as would cause the fluids to change phase at surface pressures, but this is merely an expression of the pressure-temperature relationship. Extremely light pressures, on the other hand, are limited by the greatly lowered boiling point, resulting in a rapid vaporization and loss of fluids. Actually, in nature, active life is limited in the higher atmosphere by low temperature and apparently by low oxygen content, but considering what low concentrations of available O<sub>2</sub> some aquatic animals thrive on, this in itself might not be insurmountable. However, unlike the combination of high pressure and low temperature, the combinations of low pressure and low temperature, with the resultant change of phase of H<sub>2</sub>O, at a fairly low level of chemical activity may be enough to check active life. Nevertheless, extreme conditions in this direction have been survived for short periods. Insects have been placed under the influence of highly efficient vacuum pumps and rapidly brought to a vacuum comparable to that of interstellar space and lived to survive an immediate return to normal surface conditions, Lutz (1929). Obviously this could only be a transient phenomena because the great moisture loss would quickly result in death.

It is evident, however, that while terrestrial animals well cover the gamut of temperature range in their normal activities, most live much closer to their minimum pressure threshold than to their maximum.

The truth of this is constantly attested by the pressures under which caisson workers survive and the relatively slight altitudes that force aviators to don masks or pressure suits.

Anaerobic organisms are all of a small size and are so presumably of necessity because of the low combustion rate to which their particularly limited metabolism is restricted.

Thus, life, as we know it, is very sharply restricted in a number of directions; by temperature, the effects incident to pressure, and oxygen, either freely supplied or broken out of the substrate. After these comes a host of others going to make up the milieu necessary for the survival of any particular form. All such life is concerned with a single though slightly variable gel-like compound — protoplasm, or as Beutner (1938) expresses it, "life, Carbon's outstanding property." The actual basic autocatalytic activity, as is pointed out by Alexander (1939), is properly only referable to "... the simplest self duplicating units — chromosomes and their constituent genes, mitochondria and possible subcellular symbionts." If there is analogous activity going on or possible in other systems of chemical and physical combination, we are not cognizant of such. Baldwin (1937) writes in italics "... that the conditions under which cell life is possible are very restricted indeed and have not changed substantially since life first began." With the extensive knowledge of life forms now available, it would seem that the terrestrial existence of non-protoplasmic life forms is exceedingly unlikely. Henderson (1913) discusses at length the unique position of carbon in this regard and Jones (1940) makes much of the tetravalence of carbon atoms.

If we consider such matters in a broader way, the question naturally arises as to the possibility of equivalent activity in physical systems covering quite other ranges of temperature. Obviously, what we call life is either a unique phenomenon of a very tiny temperature range, or it is not. Many doubtless would consider it mere foolishness to speculate on other possibilities. However, a consideration of various features of it, at the very least, makes it possible for us to obtain a better understanding of the peculiarities of life activities in the range in which we know it exists.

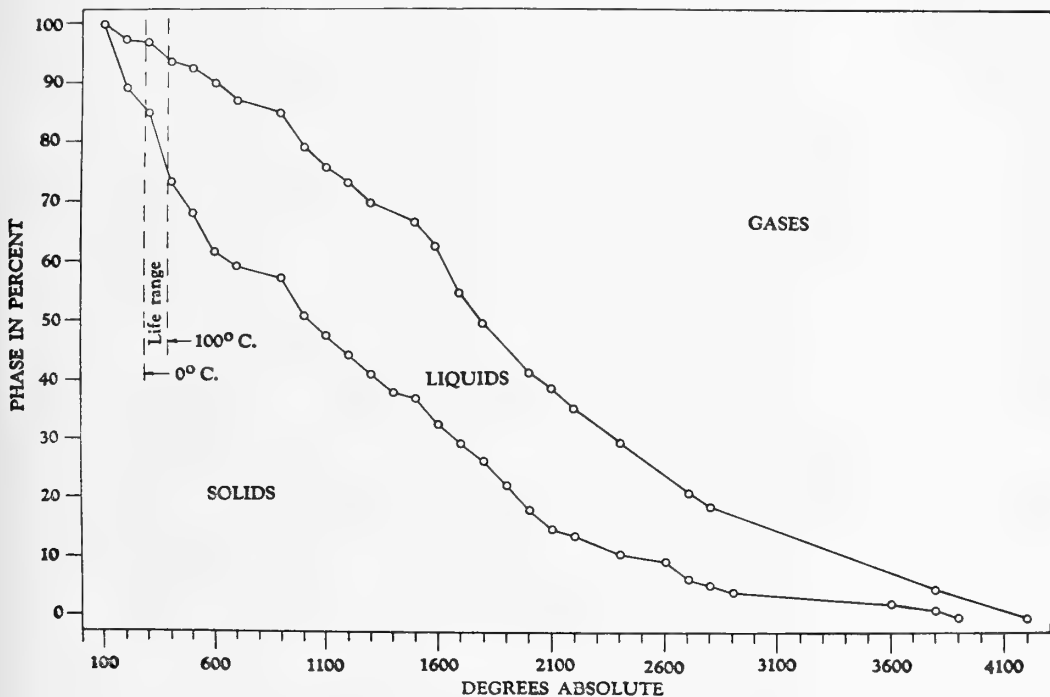
As a starting point, for a basic requirement, there must be solids, liquids and gases present in some specific temperature range if the inhabitants are going to be sufficiently like known life forms to be called equivalent or analogous. Thus the higher one goes on the temperature scale, the fewer solids and liquids and the more gases there will be found until that point is reached

where only a state of highly excited ions exist—a state of complete incandescence. Descending, more and more solids are found and less and less liquids and gases, until absolute zero is reached where no chemical activity is possible.

If the melting and boiling points of the elements are plotted, they form a regularly ascending series from absolute zero. If the phases of the elements are expressed in terms of percentages, a chart, as in Text-figure 1, may be constructed. It will be noted that our life range is very close to absolute zero as compared with the whole scale. These remarks consider only the elements. A study of the possible compounds, which would be of great importance, is a task before which a corps of physicists and chemists might well quail. However, it would appear that the various compounds possible at the different temperature levels, because of the statistical nature of the known and expected possible combinations of elements, would all go to produce curves not dissimilar in form to those obtained for the elements as shown in Text-figure 1.

In connection with a consideration of the

distribution of phases represented in various temperature ranges, the relative abundance of the separate elements enters as an item of considerable importance. Since oxygen, nitrogen and hydrogen occur on Earth in considerable quantities, it is possible for large amounts of water and an atmosphere comprised mostly of oxygen and nitrogen to be present when the suitable temperature range and other features have appeared. It would, on the other hand, be impossible to have an atmosphere in which large quantities of krypton were present. If an organic system were to be based on an environment of some of the less abundant elements it would be seriously restricted. Two conditions can be conceived. One would be such that the important materials were widely spread but highly dilute, placing the need of great effort and consequent strain on any energy exchange system so based and in this manner limiting it sharply. The other would be that the needful materials were concentrated at some focal point and there be relatively abundant. This would restrict such a system on a geographical or spatial basis. Until some hypothetical conditions at an-



Text-fig. 1. Phases of the elements at temperatures from 0° to 4200°. The temperatures, expressed in terms of absolute degrees, are grouped in classes of 100° each and the index figures read as the higher limit. Thus 100 should be read as from 0° to 100° absolute. The phases are expressed in terms of percent. of the total number of elements. Due to certain chemical features such as sublimation and the fact that complete data are not available for every element, there are some minor difficulties in the construction of such a chart, but these in no way destroy the basic nature of the curves as shown. See text for an explanation of "life range" as here indicated.

other temperature range have been postulated in some detail, to which are to be fitted some equally hypothetical creatures, it is pointless to pursue the item further. The studies of Goldschmidt (1937) on the known distribution of elements in the Earth's crust would seem to be fundamental to any such consideration. See also Russell (1941).

While it is sufficiently obvious from the above that the quantities of individual elements present would have a limiting influence on energy exchange systems of various hypothetical kinds, there could be conceived very definite mechanisms. Although such basic building blocks to known life as nitrogen, carbon, oxygen and hydrogen are sufficiently abundant, it should be remembered that many of the less common elements are needful to the present life on Earth. Iodine, for example, an important element in the living processes of many forms, is not an abundant substance. Furthermore, according to Clarke (1924), the only elements that are represented by more than one percent. of the terrestrial elements are oxygen, silicon, aluminum, iron, magnesium, calcium, sodium and potassium, in the order named. For the first listed he gives 49.2%, descending to the last with 2.4%. All are found in organisms but most are not present in a massive sense. On the other hand, carbon in this list shows only 0.08% and nitrogen, 0.03%. It is thus clear that in the present life system some of the basic materials are comparatively rare. The discussion of Goldschmidt (1937) on the mechanics of concentrating influences on the rarer elements is especially pertinent in this connection. See also Lotka (1925) for further discussion of the relative abundance of elements, their distribution and especially their availability, concentration and circulation.

Thus far we have not mentioned that other important element in the maintenance of living systems—radiant energy. It is hard to conceive of a hypothetical system without a primary or secondary source of some radiant energy as a prime mover. Since astronomers have given us a great amount of spectrographic data on radiant energy, not only in the Milky Way but from far off nebulae, for our purposes, at least, it is safe to speculate on the gamut of wave lengths sprayed out into the universe. Their relative similarity is perhaps their most striking feature. The effects on other systems, for example, the transparency and fluorescence of various substances to differing wave lengths and related matters, is too complex to be entered upon casually and would not be sufficiently significant at this point.

With these items in mind, we can make a few tentative propositions of what life-systems, if they are to be analogous, would require at any temperature-pressure range.

1. The lower the temperature the greater the variety of solids available for body-building, while the higher the fewer and more limited these would be.

2. Inverse to this would be the variety of fluids and gases for the seas, atmospheres, and body fluids, with an increase in kinds and complexities with increased temperatures.

3. The range of the temperature-pressure relationship would have to be such as not to change the phase of the body structures except in a manner analogous to that for protoplasmic life.

4. Radiant energy would have to be such as to maintain a source of prime moving force and the systems would have to be able to utilize it directly or indirectly without self-destruction.

5. Some system of energy exchange by continuous chemical activity would have to be possible in any milieu imagined.

6. With these elements the origin of life forms would be presented with the same basic problems already discussed for life on Earth. Speed of development and evolution (chemical activity) would be slower in each successive lower temperature range. Thus the length of time required for each cooler period would have to be progressively longer for complex entities to develop.

It should be clear that transfers from one temperature level to another, in an evolutionary sense, could hardly be conceivable. In connection with this, it is apparent that protoplasmic life would be nearly the last, or the last, of such a hypothetical series. In other words, our temperature range is close to the lowest at which it is easy to conceive of such activity (see Text-figure 1). This is for two reasons: (1) so many substances are locked up as solids, limiting the possible liquid and gaseous environments, and (2) the level of energy is so close to complete entropy that the activity is necessarily of a low grade in a purely chemical sense.

Stated another way, the foregoing should make it clear that life is either a unique event not far preceding a full heat death, or it is near the end of a succession of similar phenomena that occur in a series of focal points as non-connected modes along a descending temperature scale. It may be emphasized that each range of such activity would have no bearing on the next lower one, any more than the previous chemical combination of a substance bears on any further combinations it may enter as impelled under physical changes.

Since the Earth supposedly existed at a temperature too high for protoplasmic life prior to its present condition, the question naturally arises as to the existence of a



previous similar activity at a slightly higher temperature, and if such may have existed, what are the chances of finding some evidence of it. Since we have no idea as to what range such a thing might have occupied, for sake of illustration we might take the range of  $500^{\circ}$  to  $600^{\circ}$  absolute. This is equal in span of temperature to our life range, but not far above it—perhaps not far enough to be fair to the thesis. It has been selected at random for purposes of illustration but, nevertheless, an examination of the condition of the elements is of interest. Instead of about seventy-eight percent. of the elements being solids, about sixty percent. would be solids. There would be about twenty-seven percent. liquids as against our fifteen percent. and gases would be about thirteen percent. as against our seven percent. For example, the following solids in our life range would be liquids: selenium, lithium and sulphur, while iodine and bromine would always be gases. Various elements between the range of  $500^{\circ}$  and  $600^{\circ}$  would change phase as various points were passed. For example, cadmium, thallium and bismuth would melt and freeze while certain forms of phosphorous would boil and condense. Lead would occur as a liquid in very hot regions, for it melts at  $600.4^{\circ}$ , and in the presence of other substances (fluxes) below that value.

In a world so conceived, what chance of fossil survival would its "organic" remains stand on a drop to present temperatures? What is known of igneous rocks, their crystalline structures, consolidation and metamorphosis would certainly seem to preclude the survival of any structural entity frozen to our relative frigidity. Our earliest fossil-bearing rocks are so clearly of present temperature ranges that we simply cannot look hopefully to such sources for evidence.

The great variety of carbon compounds known to man and the theoretical possibility of stupendous numbers of others leads Beutner (1938b) to consider life a peculiar property reached by the proper combinations of that element. Silicon has been frequently suggested as a conceivable alternate, within our life temperature range, largely because of its comparable ability to build a large number of compounds. This has been most recently discussed by Jones (1940). Silicon, it may be noted, is not so involved in energy exchange systems of which we have knowledge. While not being disposed to debate the unique position of carbon, we may submit that a mere multiplicity of "building blocks" does not necessarily mean that an endless variety of structures will actually be built nor that a comparatively few types of building blocks preclude construction. Actually there are relatively few of the many known carbon compounds to be found in living en-

tities although surely there are many more present not as yet recognized.

Beutner himself seems to be largely concerned with the ingenious devices of Butschli, Traube, Leduc, Herrera, Jennings and Crile, many of which show simulated lifelike activity not involving organic compounds. Although these structures are of extreme interest in various connections, it does not seem that they are likely to throw much light on the question of the origin of life, possibly excepting the work of Herrera. Since living entities are clearly controlled by the same physical conditions that control non-living units, it should not be surprising that various arrangements can be made of non-living substances that react in ways similar to some of those observed in living entities. The elaborateness of some of these reactions is distinctly interesting and should be of aid in explaining behavior, morphological detail and pattern, but certainly not origins. The striking nature of these contrivances would seem to be limited only by the ingenuity of the experimenter and were it not for their spectacular nature would not be thought of in connection with a discussion of the origin of life any more than would be experiments which show that animal heat is comparable to inorganic combustion or that HCl in the stomach acts in a manner identical to HCl in a test tube. The models here under consideration can be seen to move or grow and are comparable to studies in locomotion or growth in a manner similar to the above suggested chemical comparisons and probably useful to an equivalent degree. It should also be clear that primarily the right chemical compounds must be obtained for "livingness" to begin. The form or movements come later, and obviously these physical aspects may be extremely various whereas the chemical nature of life, as we know it, is limited to one type of chemical system of energy exchange.

Rosett (1917), in describing his particular "design" of an artificial osmotic cell, gives an excellent evaluation of the over-emphasis and under-emphasis that has been accorded such studies by various schools of thought.

Beutner (1938a) recognizes the separate nature of morphology and "the power of self-reproduction" and writes, "Obviously, then, living organisms, according to our present conception, have two distinct general characteristics:

"1—The power of chemically transforming the material of their environment (or food material) into their own substance;

"2—The ability to develop diverse forms."

The first item is a definition for an autocatalytic enzyme and the second is clearly not a basic item in the nature of life but is

a historical statement based on what has apparently happened and which condition may be needful for long continued survival.

He considers viruses as having no morphology when he writes, "A filterable virus possesses the first general property to its fullest extent, but nothing of the second one." It might be equally well argued that its morphology is on a submicroscopic basis as indeed it would have to be, and that it possesses morphology in the sense that any molecule does, especially since the entire atomic theory is based on structure and arrangement (morphology).

#### EVIDENCES OF MODERN SCIENCE.

If we examine the evidences of modern science and not the more or less generally accepted speculations based thereon, we have to dig rather deep to obtain anything of real significance.

For the theologists' mysticism there is none at all, except wishful thinking and sentimentalism. This is not to be taken as a mere derogatory dismissal, for until the idea of extra-sensory perception can be fully disposed of, simple dismissal cannot have the full assurance formerly possible. However, if such a concept is to be even considered, it would automatically reduce to the consideration (1b) (page 132).

For the idea of life as planted, there is present-day evidence of the great resistance of spores and other living objects to extreme low temperatures and of their presence in the substratosphere. Coupled with this is the known force of radiant solar energy as a possible propulsive force. However, there is also the known destructive force of unfiltered radiant energy in interplanetary space, Lewis (1934). Planting as a cosmic accident would thus seem to have nothing whatever any longer to support it. Carbon found in meteorites has been thought perhaps to represent the remains of extra-terrestrial life forms. The nature of impact of these objects is such as to make such a source exceedingly unlikely. Elemental life forms have been claimed to be recovered from the interior of stone meteorites by Lipman (1932), but the true source of their origin is still undetermined. See Oparin (1938).

For the concept of spontaneous generations, several ideas have been brought forward. Born in the biological ignorance of early man, to explain his failure to understand the appearance of small animals, a mode long disproved, it nevertheless lingers in a modified form as a possibility. The part of chemical and physical changes in a system of mixed substances gives a point of departure on the assumption that the world is a cooling sphere. Under the influence of solar radiation with the Earth acting like a gigantic Soxhlet extractor, it is easy to

imagine life as a spontaneous event on the reaching of a certain state. Today, with the virus situation as it is, the differentiation between living and non-living seems to be largely academic, Stanley (1937, 1938a and b), Rivers (1939), Hunt (1939) and Martin and Fisher (1942). It is to be emphasized, however, that viruses or even unicellular units may not in the least be primitive, but may just as well, so far as present evidence goes, be derived from the products of living metazoan bodies, Breder (1936). Even if Oparin's broader views are accepted, viruses would not necessarily have to be considered as primitive. However, this may be, whether viruses came first or last, or all the way along the line, there is no really objective line of demarcation.

It is not necessary for us in the present discussion to go into a close consideration of the steady state which life represents or the electric fields which surround such units of electro-chemical activity. The work of Northrop & Burr (1937) may be noted, in passing, as indicative of this field of approach to the basic nature of livingness.

No matter what restrictions or modifications must be made, the terrestrial water circulation acts basically like a Soxhlet extractor and strongly influences the present chemical composition of the ocean, Lotka (1925). That the blood plasma of animals is not very divergent from it in a chemical sense, and protoplasm itself is clearly related, makes only a small leap of imagination necessary to assume a relationship. It has been argued most recently by Macallum (1926) and Beutner (1938b) that the first land animals may have simply carried some of their earlier aquatic environment along with them. This would seem to be too pat a statement, for it would seem that if oceans and organisms are all part of one evolving chemical system, it would be quite natural for both to partake of considerable chemical similarity. Redfield (1934) gives some very suggestive data in this connection. This resemblance of organisms would naturally be to a fluid in which there was considerable matter in solution rather than to the solid substrate or to fresh water. The osmotically low value of fresh water, if nothing else, would hardly be friendly to the consolidation of a primitive gel. See Pantin (1931) and Baldwin (1937). Croneis & Krumbein (1936) discuss the hypothesis of Chamberlin to the effect that life may have originated in soil, largely on the basis of the dispersive effects of oceanic conditions. Under water, subsoil conditions would seem to obviate the principal objection. Perhaps the primordial gel was interstitial in the sands of early beaches, an arena of life now occupied by many specialized forms, and which only recently has begun to receive the attention of biologists that it undoubtedly deserves.

The above remarks apply equally well to either a normal chemical evolution or a rare "accident."

#### EFFECTS ON SCIENTIFIC THOUGHT.

The main purpose of the present paper is to discuss the effect of these various hypotheses on scientific thought. The different ideas that have been advanced to explain the methods of evolution are usually given and discussed as though the origin of life had no bearing on the subject. This is certainly not the case but in evaluating the plausibility of any of them we must necessarily consider their merits against a background of what origin of life is presupposed. Even in cases where there are alternates, the one selected causes certain strictures or produces certain effects implied in all reasoning derived therefrom.

The primary forms of organic transformation that have been suggested by biologists may be reduced to four basic concepts:

(1) Inheritance of acquired characteristics (Lamarckianism), now discarded because of the failure of experimental evidence.

(2) Natural selection in the Darwinian and neo-Darwinian sense and more or less under critical appraisal.

(3) Orthogenesis, perhaps, not susceptible of scientific investigation by direct methods.

(4) Mutation in the DeVriesian sense or in the modern version of Goldschmidt (1940) involving violent and sudden transformations.

All other views seem to be variants or combinations of the above four, more frequently differing in terminology than in content. See Dobzhansky (1940).

Before discussing these varying views in detail, the number of points of origin of life, which also has a marked bearing on the whole question of organic relationship, may best be examined.

Considering monophyleticism versus polyphyleticism, it should be clear that if the latter is implied by the nature of the origin assumed, it is pointless to attempt to build phylogenetic trees that try to tie all forms together. Since most present-day biologists, tacitly at least, imply a monophyletic origin, it must mean that some of the previously discussed ideas of life genesis have been discarded by them. It is evident that while a monophyletic origin may be considered for all concepts, since life on earth must have commenced at least once, such is not necessarily true of every concept. Stated another way, polyphyleticism is possible only if life origin is part of a normal process (planted or spontaneous). While this could also be monophyletic, the assumption of a

rare "improbable" chemical "accident" or planting would almost certainly preclude polyphyleticism.

With the "normal" processes of chemical evolution, an orthogenetic basis of evolution would certainly be expected—simply as a mere continuing of a spontaneous activity. With the planted processes, either repeated or rare, or with a rare chemical accident, it might or might not be expected. In other words, any of the conceivable sources of life could carry with it the possibility of some orthogenetic scheme "built into" organisms. Under such a scheme there would be nothing to prevent the possible occurrence of mutations in the Goldschmidt sense. In fact, it might well be that such should be expected and thought of roughly as somewhat analogous to the change of phase in inorganic "orthogenetic" systems occurring when certain points of development have been reached. This concept is, of course, not unlike that of the emergent evolution of C. L. Morgan (1923).

Natural selection in the coarsest sense would no doubt operate from the first. Whether it carries over into the refinements generally expected of it is another matter, but one on which the present discussion may be suggestive. If organisms have some such orthogenetic "program" built into their beings, it is certainly not surprising that neo-Darwinians have much trouble in trying to explain natural selection on a micrometric basis.

Adaptation, in the teleological sense, these thoughts do not tend to support, since the organic units must by random or other means find themselves in environments in which they could continue as such. Here again only the coarse effects can be argued for with any strength. All others could be just as well accounted for by some straight process of orthogenesis in which the primary organisms either found themselves in an environment sufficiently suitable or perished if they did not.

It is of more than passing interest in this connection that Spencer & Melroy (1942), on a basis of their results on exposing bacteria, protozoa and flat worms to carcinogenic agents through many generations, wrote, "The biological generalization that certain environments may be ontogenetically harmless but phylogenetically lethal is suggested."

This should not be interpreted to mean that organisms are not affected by their environment except to survive or perish. However one may care to try to account for the interesting associations of highly specialized organisms of today with their environment, these refinements certainly appeared at a relatively late date in phylogeny unless one wishes to assume that this feature of evolution is an inherent property of organisms.

If it is, it is rather amazing how many animals have lost the faculty of transmitting environmental effects (acquired characters) at least quickly, and how well they manage without it. This thought is, of course, related to the complete inability of any one to establish satisfactorily the inheritance of acquired characters.

The well-known habit of flounders of quickly matching their background in considerable detail may be considered a matter of individual behavior. This operates, and presumably without conscious effort, through sense organs (the eyes) but is in truth no more remarkable than the fact that we stand on two legs without conscious effort. Very possibly a flounder on a wrong background is as uncomfortable as we are when out of plumb. Since any creature *necessarily* is limited to the equipment it is endowed with, it normally makes use of such as it has and survives or not, according to the results obtained. This, of course, is a far cry from the implications of the adaptationists who for long have certainly over-played the niceness of fit between organism and environment and have failed conspicuously to explain the development of complex organs, such as eyes, for example. That it is at least possible for flounders to reach sexual maturity without benefit of the usual color matching changes has been shown by Breder (1938). His fish may have survived on a purely random chance or it may have consistently kept its conspicuous coloration out of sight by more adequate burial than is usual to the species.

All this obviously implies that what an animal does with its equipment is considerably superior to what particular kind it has, in a functional sense. The divergence of the forms of organisms can certainly be used to support this view as well as the essential basic similarity of what they all do. What it does is more closely associated with the restrictions of environment than what it has. Stated another way, a Mammoth can be frozen in the Arctic tundra for generations and essentially retain its form outside of temperature ranges at which it can do anything. Or again, an insect might have its form changed (and be ruined) by being caught in the beak of a bird. It could be saved from this by flying away (if it had wings), crawling between grass blades (if it had none), or even just by sitting very still. This is merely fitting its activity to its morphological limits to suit its environment. That these morphological limits may be exceedingly various is evident from the above—but what it does must fit its needs much more closely; thus a long-legged and a short-legged insect may find shelter beneath the same leaf. It is little wonder that the “fitness” and lack of “fitness” of animals to

environment as based on morphology have given rise to endless discussion.

Returning to the basic argument, however, it should be clear from the preceding, without laboring the point, that before such activity can take place at all the primitive organic entity must first fit its environment in a purely physiological sense. The temperature thresholds that hem in our kind of life are clearly first in physiological importance and these must be substantially maintained long before adjustments between one animal and another can even be conceived. The losses of species due to glaciation and other major changes so far overshadow micro-adjustments that one is forced to wonder at their alleged importance. If an orthogenesis could be established, all the observed results could be reasonably explained, whereas the reverse cannot be said for the usual concepts of pure natural selection and other similar ideas.

Finally, the thoughts here expressed lean strongly to the conception of life origin on Earth as a physico-chemical evolution of the sort conceived of by Oparin (1938). This inevitably carries with it a strong bias to orthogenesis, places emphasis on the fundamental limiting factors of life, on the importance of what an organism does with its equipment rather than what equipment it has, and questions the micrometric functioning of selective processes. Furthermore, in an evolving physico-chemical system in which one reaction follows another, no one would think of referring to the disappearance of some compound, as the result of this activity, as natural selection. Only when such become sufficiently complicated and individuated does this word put in its appearance (biological literature) and in this sense would seem to be reducible to the status of a convenient phrase to hide behind. Lotka's (1925) chapter on “the statistical meaning of irreversibility” is very suggestive in this connection as is the physico-chemical determinism of Alexander (1939).

The function of reproduction in connection with this problem is far from clear. Oparin (1938), in spite of his interesting discussion of coazervate systems, becomes somewhat vague at this point. Since it is one of the generally obvious basic differences between the animate and inanimate, it is in serious need of further critical study from new approaches. Perhaps here, after all, lies the key to the secret of life and what may be responsible for the effects that have given biologists so much trouble of interpretation. Since viruses apparently do not have need for the elaborate mechanisms of reproduction to be found in the larger life forms, it may well be that the entire business of both sexual and asexual reproduction is a means of circumventing the re-

stricting influences of elaborate morphological structure, a need that does not arise so long as the naked enzymes have no more than molecular structure with which to deal.

If we consider life as a retardation of a general increasing entropy it follows that by the peculiar nature of living processes we have in effect a building up of a certain amount of back pressure to the degradation of energy. This, so far as we know, always occurs in individuated clumps of heterogeneous matter—the individual of the biologist. This goes on for a time and finally the individual disintegrates. From the first, all such individuated organizations are fighting a losing battle against the general downward trend of available energy, which is evidently bound to culminate in death. This places reproduction in the role of casting off new colonies of such aggregates of material—like a long relay race up a down-moving escalator. Whether this necessarily culminates in the eventual loss of the race and the generally accepted heat-death is still not clear, at least for our little niche in the space-time frame. *A priori*, there seems to be no particular reason for things working just that way, for surely it is conceivable that some sort of energy exchange system could be imagined that would not necessarily exhaust itself in a short time, passing on only a tiny fragment saved from the forces of destruction, if it were not running a breathless race up a down-escalator.

These ideas lead naturally to a piece of pure speculation that it is tempting to indulge in and which really is at the heart of the perhaps seemingly unconnected items that comprise this paper. If we visualize all known items within our universe as a simple expression of physico-chemical activity, as a part of an increasing entropy, it is clear from the preceding that we are very near the end, in a cosmic sense. Life, as we know it, appears well along to the end and gives the appearance of a manifestation that seems to give back pressure to the common lowering of energy levels. Up to the appearance of autocatalysis all activity would run along well enough according to the straightforward operation of the Second Law. Finally the autocatalysts emerge into ex-

tremely complex individualized units possessing tremendous urges to run counter to the forces of their surroundings, which urges are more and more forceful as that strange element "consciousness" appears. Finally we reach the stage of present man with his deliberate, elaborate and more or less successful attempts to modify his environment. With this has come careful, though blundering, thought processes attempting to understand what it is all about, purely emotional at first but grading finally into an intellectual and objective plane. One wonders if this drive is a new one directed against the continuing entropic drift similar to but superimposed and of a later order than the fundamental sex drive that seems to be the final difference between the inert drift downward of the non-living and the hold-back of living entities. Looked at this way, there is little wonder that such operations are a source of trouble and a general preoccupation.

This, of course, is as far as we can see, as it is the level of activity at which we now cut off. What then of the future? Two possibilities seem to appear. First that the life activity merely peters out sooner or later, and it is in truth just one hold-back on a descending energy scale (and there may have been others, as already suggested) and will pass on with the universe to complete entropy. Secondly, it may be that life activity is of more importance than reason dares permit us to postulate. The present activity of man one may speculate upon as part of the physico-chemical evolution now going on but inducing a progressive retardation in the otherwise increasing entropy. This could conceivably result in one of two fashions. One would be an increasing slowing of the process as entropy approaches the absolute. In other words, the evolution of such a physico-chemical system could be expressed by a curve reaching an asymptote. The other would be a complete reversal of trends, perhaps brought about by the "intelligence" of some groups of individuated bits of matter in which case the curve might be something in the form of a parabola, a hyperbola or, fantastically, even a closed figure.

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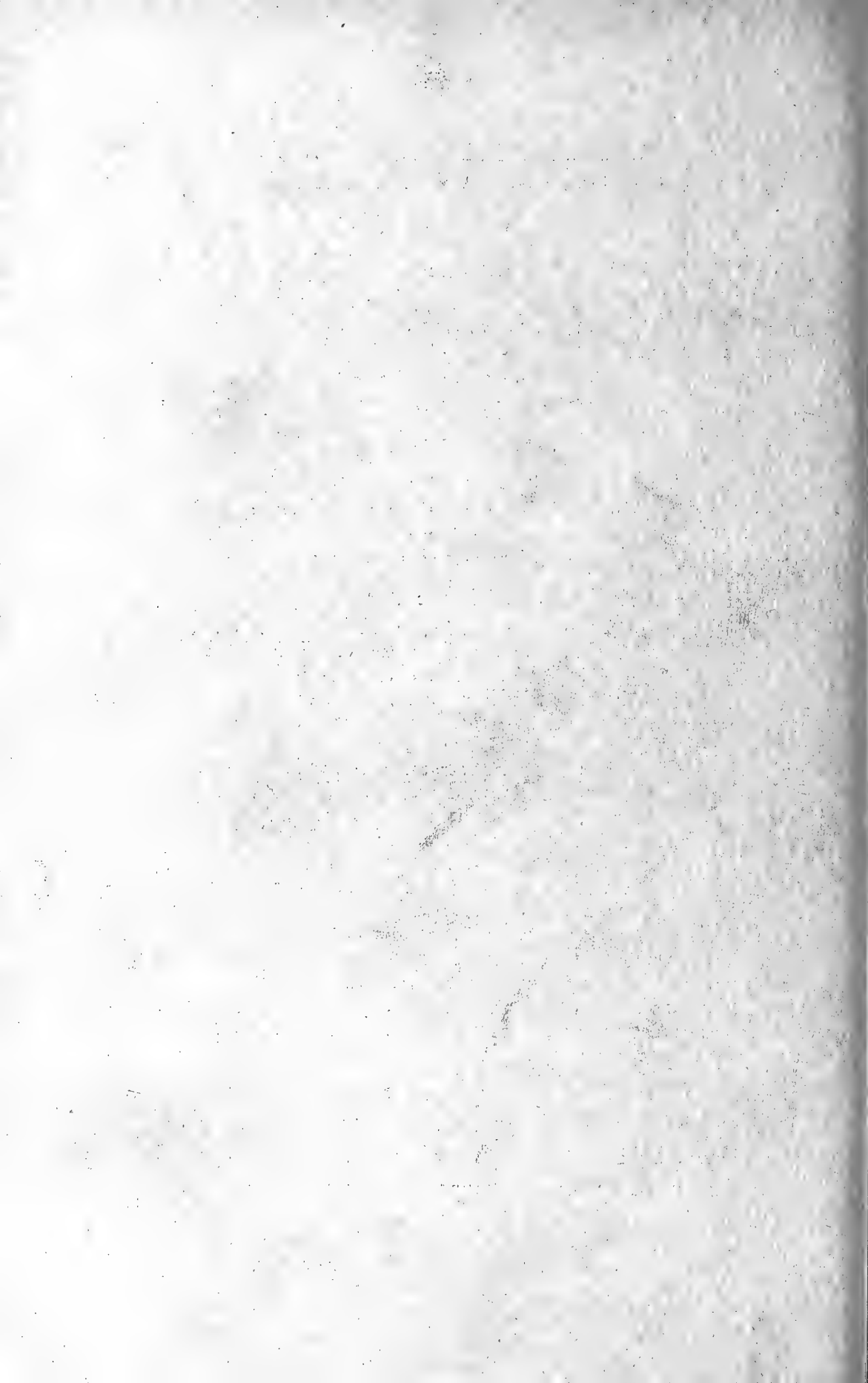
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## 1.

## Biometry of Puffers and Their Parasites.

ROSS F. NIGRELLI

&amp;

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New York Zoological Society

## INTRODUCTION.

In connection with other investigations of the New York Aquarium, studies were made of fishes and fish parasites indigenous to Sandy Hook Bay, N. J. The fishes of this area have been thoroughly studied by Breder (1923-1939) and his collaborators. Among other species, the northern puffer or blowfish, *Spheroides maculatus* (Bloch & Schneider), is found there in large numbers from June to September and is collected in these months for exhibition purpose.

A routine check for parasites is made on all fishes that eventually will become part of the Aquarium's exhibition. In the course of these investigations it was evident that puffers were the foci for infestations that were responsible for mortalities of other and more valuable species of fishes. For this reason, it was decided that a survey of their parasitic fauna would yield additional information in this regard and that perhaps such a study would suggest methods for their control.

## SAMPLINGS.

A random selection of puffers was made when the specimens were brought into the Aquarium from the pound nets in Sandy Hook Bay. A total of 294 fish was taken, varying in size from 2 to 24 cm. In Table I the number of individuals collected in the months from June to October, inclusive, for the years 1938, 1939 and 1940, are shown. The largest number of puffers was caught in September for the three years. Table II gives the numbers of each sex collected during the same period. 49% of these were males; 44% were females; 7% were immature. The males varied in size from 10-20 cm.; females from 11-24; immature puffers measured up to 12 cm. In this collection, fish 21 cm. or more were females. This distribution is shown in Table III and agrees with the data given by Welsh & Breder (1922) for puffers caught off Atlantic City, N. J. The only difference noted

is the slight extension for the mature forms in both the upper and lower size limits, the result of a larger sample.

## ANALYSIS OF THE INTESTINAL CONTENTS OF PUFFERS.

The intestinal contents of puffers were examined by Linton (1901, 1905) from Woods Hole, Mass., and Beaufort, N. C., and by Welsh & Breder (1922) from Atlantic City. These investigators found that the puffer's diet consisted of minute crustaceans, crabs, shrimps, bivalve and univalve mollusks, annelids and sea-weeds. In addition to such items, fish was also part of the diet of Sandy Hook puffers.

It was Ward (1908) who stated that "The parasitic fauna of any animal is primarily a function of its habitat" and, one may add, of its eating habits. A knowledge of the food cycle is very important, often revealing the source of internal parasites. Thus, for the five trematodes reported in this paper (see Table IV), the infective stages are to be found in mollusks, crustaceans and fishes. Martin (1939) showed that in the case of *Stephanostomum tenue*, one of the intestinal flukes of the puffer, the cercariae develop in the snail, *Nassa obsoleta*, and the metacercariae are found in the spearing or common silverside, *Menidia menidia notata*. The spearing is a small fish occurring in great abundance along our coast and is usually preyed upon by larger fish. It is not surprising, therefore, to find this species of fluke living in a large variety of definitive hosts.

In the life-histories of *Lecithaster* and *Podocotyle* (see Hunnien & Cable, 1941 a and b), the cercarial stages appear in certain snails and the metacercariae or infective forms occur unencysted in copepods and amphipods. Since these minute crustaceans are part of the diet of many marine fishes, it is to be expected that no host-specificity is shown by these trematodes. The cycles of *Bianium* and *Lintonium* are still unknown but they are almost certain to follow one of the patterns indicated above.

## PARASITES OF THE PUFFER.

## A. External Parasites.

Insofar as could be determined, about 18 species of parasites have been recorded from the puffer. Thirteen of these were found in Sandy Hook Bay fish and are listed in Table IV.

The small opercular opening, characteristic of puffers, encourages the concentration of ectoparasites in the gill chambers. In regard to pathogenicity, ectoparasites of fishes are the most important ones to consider for invariably they cause death of the host if sufficient numbers are present.

TABLE I.

Number of Puffers Collected,  
According to Dates.

Month	1938	1939	1940	Total
June	7	6	12	25
July	—	15	69	84
August	20	20	19	59
September	39	54	30	123
October	1	2	—	3
Total	67	97	130	294

The dinoflagellate, *Oodinium ocellatum* Brown, is recorded from only two fish in this report but in previous years (1935-1937) it was the cause of mortality of various marine fishes (tropical and temperate) kept in captivity. The life-history of *Oodinium* was demonstrated by Nigrelli (1936) and it was shown that the epidemic in the Aquarium was centered in puffers and spiny boxfish brought in from Sandy Hook Bay.

The two species of *Trichodina* were described recently by Padnos & Nigrelli (1942). Heavy infestations of these ciliates will cause death. Nigrelli (1940) showed that puffers were the source for *Trichodina* found on other fishes in the Aquarium. That these peritrich ciliates are not limited to Sandy Hook fish is indicated by the fact that in 1939 they were also present on the gills and skin of 27 out of 32 puffers examined from Orient Point, L. I. The protozoa reported by Linton (1940) as *Cyclochaeta domerguei* Moroff (p. 23) may be *Trichodina*. If this is true, it appears

that the puffers are infected with the organism throughout its known range.

Tables V and VI show the relationship of the intensity of *Trichodina* infection to sex of the host and to the dates the puffers were taken. Fish showing an exceptionally light infection may be considered negative for it is suspected that some of the gills probably were contaminated at the time of the examinations. As will be seen later, the host-parasite relation shown here is opposite to that demonstrated for the metazoan parasites of the puffers. There is a tendency towards an increase infection in males. The intensity of the infection in all fish decreases towards the latter part of the summer. The effect of temperature has not been definitely decided. Our records show that the temperature in the bay off the Battery reaches a maximum in August and begins to drop in the latter part of the month. Table VI shows that there may be a correlation, and this is to be expected, between the temperature and growth of the ciliates. The Table also indicates that the optimum is around 70° F., for it is at this temperature that the largest number of puffers were infected. This interpretation is further corroborated by the fact that most of the reproductive stages (conjugation) of this organism were obtained from the gills of puffers caught in July and September.

A single myxosporidian cyst was found on the gills. The spores are bivalve and more or less oval in shape, indicating that this form should be allocated to the family Myxosomatidae. No specific identification was made because of insufficient material. However, since the mode of transmission is direct, such organisms must be considered as potential parasites of real importance for under epidemic conditions they could cause considerable damage to tissues (Nigrelli & Smith, 1938) and eventually result in death.

The copepod, *Pseudochondracanthus dice-raus* Wilson (see Wilson, 1932), is another important gill parasite of puffers. As many as 140 specimens were found attached to the gills of a single fish. The method of transmission is simple and direct. The fertile

TABLE II.

Number of Puffers Collected, According to Sex.

Month	1938			1939			1940			Total			Grand Total
	M	F	I	M	F	I	M	F	I	M	F	I	
June	2	5	—	2	4	—	4	8	—	8	17	—	25
July	—	—	—	7	8	—	40	29	—	47	37	—	84
August	2	4	14	10	7	3	13	6	—	25	17	17	59
September	18	21	—	28	24	2	18	12	—	64	57	2	123
October	—	—	1	1	1	—	—	—	—	1	1	1	3
Total	22	30	15	48	44	5	75	55	—	145	129	20	294

TABLE III.  
Collection of Puffers:  
Relation of Size to Sex.

Size in cm.	M	F	I	Total
2	—	—	1	1
3	—	—	2	2
4	—	—	2	2
5	—	—	1	1
6	—	—	2	2
7	—	—	4	4
8	—	—	—	—
9	—	—	2	2
10	4	—	—	4
11	10	4	2	16
12	7	9	4	20
13	13	5	—	18
14	18	4	—	22
15	21	7	—	28
16	25	7	—	32
17	20	14	—	34
18	10	18	—	28
19	14	18	—	32
20	3	16	—	19
21	—	10	—	10
22	—	8	—	8
23	—	8	—	8
24	—	1	—	1
Total	145	129	20	294

eggs hatch into infective stages (copepodid) which attach themselves immediately to the gills. It is obvious that if sufficient numbers are present on the delicate gill filaments interference with the normal respiratory function will occur.

## B. Internal Parasites.

### 1. Trematodes.

All the trematodes recovered from the puffers are digenetic. Of the five species found in the Sandy Hook puffers, *Lintonium vibex* (Linton) (Stunkard & Nigrelli, 1930) and *Bianium plicatum* (Linton) (Stunkard, 1931) are the only ones found in appreciable numbers and with any degree of constancy. They occur in the digestive tract and were present, respectively, in 66% and 67% of the fish examined.

*Lintonium vibex* appears to be species-specific. It has not been recorded from any other fish occurring naturally in the North Atlantic. Linton (1940) reported an infestation in a queen triggerfish, *Balistes vetula*, which had straggled northward to the Woods Hole region during the summer. The triggerfish probably became infected when it migrated into the northern waters. Further, this species, examined for internal parasites from its natural habitat, has not been reported as a host for *Lintonium*. Close relatives of the puffer, such as the rabbit fish or smooth puffer, *Lagocephalus laevigatus*, and the common spiny boxfish, *Chilomycterus schoepfii*, taken at Sandy Hook Bay at the same time that puffers were

seined, were free of this trematode. Both of these fish have feeding habits similar to the common puffer.

*Bianium plicatum* is usually present in puffers in large numbers. The parasite was originally described as an unidentified species by Linton in 1898 from two specimens found in the smooth puffer and the tom cod, *Microgadus codus*, and again in 1929 as *Psilostomum plicatum* from the intestine of the herring gull, *Larus argentatus*. It was shown by Stunkard (1931) that the two forms were identical with a species he had described in 1930 as *Bianium concavum*, a common intestinal parasite of the puffer and for this reason was designated *B. plicatum*. This important discovery shows definitely, what often has been suspected, that parasites which are normally found in one host may persist for a time in its predators. The presence of *Bianium* in the smooth puffer and the tom cod may be accounted for in this manner. From the record so far presented, it seems that *Bianium plicatum* also is a specific puffer parasite.

*Podocotyle olssonii* Odhner, *Lecithaster confusus* Odhner and *Stephanostomum tenue* (Linton) have been described from a variety of North Atlantic fishes. Their life-histories were discussed above, and although together they were found in 8% of the puffers, individually there were never enough present at one time to make them significant.

*Cymbophallus vitellus* (Linton) is another intestinal fluke reported for puffers from Woods Hole region. It is closely related to *Podocotyle* and like this form is found in a large number of fishes in this locality.

### 2. Cestodes.

The striking feature of the present studies is the dearth of cestodes. A single, unidentified scolex was found. Linton (1924) reported more than 24 encysted and free scoleces from about 20 puffers examined from Woods Hole. From this material he was able to identify *Rhynchobothrium bulbifer*, *R. tumidulum* and *Tetrarhynchus bisulcatus*. These identifications are incomplete because, as pointed out by Nigrelli (1938), the names *Tetrarhynchus* and *Rhynchobothrium* have no generic status. They are group names. *Tetrarhynchus bisulcatus* Linton has since been redesignated *Nybelinia bisulcata* (Linton) Dollfus. Larval cestodes occur in numerous teleost hosts and although their life-cycles are not completely understood, it is known that they become sexually mature in the spiral valve regions of the intestines of elasmobranchs.

### 3. Nematodes.

Thirty-six per cent of the puffers were infested with nematodes belonging to the genera *Contracaecum* and *Porrocaecum*. No

TABLE IV.

List of the Parasites Collected from Puffers of Sandy Hook Bay, N. J.

Parasite	Site of Infestation	M	F	I	Total	Ratio of Infect. %
1. <i>Oodinium ocellatum</i> (Dinoflagellate)	Gills and Skin	—	2	—	2	.7
2. <i>Trichodina spheroidesi</i>	Gills and Skin }	126	113	6	245	83.0
3. <i>Trichodina halli</i> (Ciliate)	Gills and Skin }					
4. <i>Myxosporidian</i> (sp. ?) (Cnidosporidia)	Gills	—	1	—	1	.3
5. <i>Lintonium vibex</i> (Trematode)	Pharynx	101	82	—	183	66.0
6. <i>Bianium plicitum</i> (Trematode)	Intestine	98	98	—	196	67.0
7. <i>Podocotyle olssoni</i> (Trematode)	Intestine	9	5	—	14	5.0
8. <i>Lecithaster confusus</i> (Trematode)	Intestine	3	1	—	4	1.4
9. <i>Stephanostomum tenue</i> (Trematode)	Intestine	1	4	—	5	2.0
10. Tapeworm scolex (sp. ?)	Intestine	1	—	—	1	.3
11. <i>Contracaecum</i> sp. (Nematode)	Body Cavity	29	30	—	59	20.0
12. <i>Porrocaecum</i> sp. (Nematode)	Intestine	24	23	—	47	16.0
13. <i>Pseudochondracanthus</i> <i>diceraus</i> (Copepod)	Gills	106	98	—	207	70.0

specific identification was made because they are difficult to distinguish from any one of a number of species reported from marine fishes. Both forms are larval in character. *Contracaecum* is invariably found coiled in delicate cysts in the retroperitoneal regions of the liver, intestine and other organs. Sexually mature stages are known to occur in piscivorous birds and mammals. *Porrocaecum* was found free in the intestine of puffers. These probably become mature in elasmobranchs, marine turtles or seals.

The acanthocephalan, *Echinorhynchus acus*, reported by Linton (1901) from the pharynx of a single puffer, was not present in our material nor has it been recorded from puffers since that time. This must be an accidental infestation.

#### EFFECTS OF INTERNAL PARASITES ON THE HOST.

There was no evidence to indicate any real pathological effects in instances of severe infestations with the internal parasites just described. The presence of large numbers of flukes must without doubt elicit some physiological response not often obvious in the course of autopsy. In certain instances it has been noted that intestinal flukes in fishes are capable of causing an enteritis (Nigrelli, 1940), excess production of mucus and a superficial necrosis of the mucus coat.

It is interesting to point out that in infestations with *Bianium*, all of the individuals appeared to be at about the same stage of development (as indicated by size), suggesting that puffers obtain a single dose. On the other hand, individuals of *Lintonium* were found varying in size from minute, hardly perceptible forms to large, sexually mature specimens. This shows that puffers become infested continuously with *Lintonium* and that an initial infestation does not confer any resistance to the host. Whether or not the one infestation with *Bianium* is sufficient for puffers to develop an immunity against a further attack of this parasite is not known. That the infestation is less stable than that of *Lintonium* is demonstrated by the observation that puffers subjected to a period of captivity lose most or all of the *Bianium* while *Lintonium* may persist indefinitely.

#### OCCURRENCE OF PARASITES OF PUFFERS ACCORDING TO DATES OF CAPTURE.

Table VII summarizes the data regarding the number of parasites collected from the 294 puffers examined. As may be seen, the intensity of infestation reaches a peak in July and sharply drops off in August. For the first two months, 109 fish were examined in the three years from which 5,022 specimens of the three species were counted. In the last three months 185 fish examined yielded only 1,328 parasites. Although 25%



TABLE V.  
Intensity of *Trichodina* Infection in Relation to Sex.

Intensity of Infection*	Male	Female	Immature	Total	%
Exceptionally Heavy	7	8		15	
Very Heavy	5	10	1	16	
Heavy	18	18		36	23.00
Medium	9	6		15	
Light	29	29	1	59	
Very Light	19	20	3	42	39.00
Exceptionally Light	39	22	1	62	
Negative	19	16	14	49	38.00
Total	145	129	20	294	100.00

\* *Exceptionally Heavy*, too many in the field to count; *Very Heavy*, about 100 ciliates in each field; *Heavy*, about 50 in each field; *Medium*, about 25 in each field; *Light*, about 12 in each field; *Very Light*, 1 or 2 in each field; *Exceptionally Light*, 1 or 2 in an occasional field. Note: Some of the last mentioned may be contamination.

more fish were examined during the latter period, the parasite fauna was 60% less. It should be indicated here that during June and July all females examined were gravid while most fish caught in August and September had spawned. The great decrease in the numbers of parasites, during the latter period, as shown below, may be attributed partly to the spawning activities of the fish.

OCCURRENCE OF PARASITES IN RELATION TO SIZE AND SEX OF PUFFERS.

Table VIII shows the total number of parasites, excluding the protozoa, in relation to host size. It will be seen that the number of parasites increases rapidly with the size and age of the fish. Conversely, puffers up to 10 cm. in length were particularly free of parasites. A total of 6,520 parasites were counted. 66% of these were taken from female puffers, although there were fewer females than males in the total catch. This does not necessarily mean that females are more susceptible because of their larger size. Table IX shows the relation of the infestation to sex, according to dates the fish were caught. In this series a total count of the three major parasites was made. The figures show that the fe-

male puffers are susceptible to heavier infestations. This is partly corroborated by the data given in Table X showing fish infected simultaneously with the three major parasites. It will be noted that in puffers measuring from 16-19 cm., inclusive, the number of males and females collected was about equal (33 and 32 respectively), yet the females had at least 50% more parasites than the males. The greater susceptibility of females to parasitic infestation may be attributed in part to their more intensive feeding preparatory to spawning. This Table also shows that *Bianium* is present in larger numbers.

PUFFERS SIMULTANEOUSLY INFESTED WITH THE THREE MAJOR PARASITES (EXCLUDING PROTOZOA).

An analysis was made to determine whether or not a heavy infestation of one kind of parasite would confer on puffers a certain amount of resistance to other types. Table X shows that this does not happen. About 45% of the fish were simultaneously infested with *Pseudochondracanthus*, *Lintonium* and *Bianium*. Furthermore, this 45% was infested with about 84% of these parasites.

TABLE VI.  
Intensity of *Trichodina* Infection in Relation to Dates.

Month	Av. Temp.*	Heavy to Except. Heavy Infect.	Medium to Light Infect.	Except. Light to Neg. Infect.	Total
June	63.0F.	10	10	5	25
July	68.0	23	33	28	84
August	72.0	8	20	31	59
September	70.0	25	53	45	123
October	66.0	1	—	2	3
Total		67	116	111	294

\* Average temperature in Bay off Battery Park for years 1938, 1939, 1940.

TABLE VII.  
Number of Parasites Collected (Three Species Only), According to Dates.

Month	Copepod	<i>Lintonium</i>	<i>Bianium</i>	Total
June	219	129	1108	1456
July	917	433	2216	3566
August	195	192	263	650
September	161	248	268	677
October	—	1	—	1
Total	1492	1003	3855	6350

TABLE VIII.  
Size of Host and the Total Number of Parasites Collected from Puffers  
(Excluding Protozoa).

Size in cm.*	Male	Female	Immature	Total
2	—	—	—	—
3	—	—	—	—
4	—	—	—	—
5	—	—	—	—
6	—	—	—	—
7	—	—	—	—
8	—	—	—	—
9	—	—	2	2
10	62	1	—	63
11	151	1	1	153
12	111	55	4	170
13	132	198	—	330
14	175	65	—	240
15	199	92	—	291
16	265	38	—	303
17	327	190	—	517
18	230	698	—	928
19	493	784	—	1277
20	86	573	—	659
21	—	713	—	713
22	—	442	—	442
23	—	331	—	331
24	—	101	—	101
Total	2231	4282	7	6520

\*Standard length

FREQUENCY DISTRIBUTION OF PARASITES  
OF PUFFERS, EXCLUDING PROTOZOA,  
(CONSIDERED IN GROUPS OF 25).

Table XI shows the frequency with which certain numbers of parasites occur in puffers when considered in groups of 25. As may be seen 11% of the puffers were free of infection. 63% of the fish had from 1-25 parasites. Fish with more than 100 parasites were all females. However, they comprise only about 3% of the catch.

SUMMARY AND CONCLUSIONS.

1. The parasitic fauna of puffers from Sandy Hook Bay, N. J., were studied.
2. Two hundred and ninety-four fish were collected in the months from June to October inclusive, for the years 1938, 1939, 1940. The largest number of fish were caught in September for the three years.
3. The size range of the host extended from 2-24 cm. Fish 9 cm. or less were

immature, although they may reach a length of 12 cm.; males measured from 10-20 cm.; females from 11-24 cm. Puffers 21 cm. or more in length were all females.

4. Food eaten by puffers consists of copepods, amphipods, crabs, shrimps, bivalve and univalve mollusks, annelids, fish and sea-weeds. The life-cycle of internal parasites, particularly the flukes, involves any one of these as intermediate host.
5. Thirteen kinds of parasites were found: 4 species of protozoa, 5 species of digenetic trematodes, 1 tapeworm, 2 nematode species and 1 copepod. The protozoans and the copepods are gill parasites, heavy concentrations of which will cause death of puffers and other marine fishes.
6. In reference to numbers, the important metazoan parasites of the puffer are the flukes, *Lintonium vibex* and *Bian-*

*ium plicatum*, and the copepod, *Pseudochondracanthus diceratus*.

- 7. Both *Lintonium vibex* and *Bianium plicatum* are specific to puffers of the North Atlantic coast of the United States.
- 8. Fishes related to the puffers (rabbit fish and queen triggerfish) migrating into this area may become infested with these flukes. However, other relatives of puffers, such as the spiny boxfish, living in the same area and apparently with the same feeding habits, seem to be resistant to *Lintonium* and *Bianium*.
- 9. From observations, it appears that puffers are infested continuously with *Lintonium* while in the case of *Bianium* only one infestation occurs at a time.
- 10. In captivity, the puffers lose their *Bianium* after a short period while *Lintonium* may persist indefinitely.
- 11. Other species of flukes recovered from Sandy Hook Bay puffers have also been reported from a large variety of fishes of the North Atlantic. In some cases,

these parasites may be accidental infestations.

- 12. Although a number of species of cestodes have been described from puffers, only a single unidentified scolex was recovered from Sandy Hook Bay fish.
- 13. The two species of nematodes found were larval in character and presumably sexually mature forms come up in piscivorous hosts.

TABLE IX.

Number of Parasites Collected (Three Species Only), According to Sex.  
Total for the Three Years

Month	Male	Female	Total
June	374	1082	1456
July	1267	2299	3566
August	221	429	650
September	283	394	677
October	1	—	1
Total	2148	4204	6350

TABLE X.

Puffers Infested Simultaneously with the Three Major Parasites (Excluding Protozoa).

Size in cm.	No. of Individuals in each class	M	F	I	Copepod	<i>Lintonium</i>	<i>Bianium</i>
10	4	3	—	—	43	4	15
11	16	5	—	—	27	26	51
12	20	2	4	—	67	34	31
13	18	3	4		59	8	100
14	22	4	—		48	45	42
15	28	6	3		58	42	105
16	32	8	1		66	23	93
17	34	8	5		90	72	261
18	28	7	11		89	135	513
10	32	10	15		205	190	697
20	19	3	9		83	72	424
21	10	0	8		85	33	565
22	8		6		189	30	205
23	8		6		46	34	202
24	1		1		5	1	93
Total	280	61	71	—	1160	749	3397

TABLE XI.

Frequency Distribution of Parasites of Puffers (Excluding Protozoa). In Groups of 25.

Number of Parasites	Male	Female	Immature	Total	Percentage
0	7	7	17	34	10.54
1-25	105	76	3	184	62.65
26-50	25	21		46	15.64
51-75	6	9		15	5.10
76-100	2	8		10	3.43
101-125	0	2		2	.68
126-150	0	0		0	.00
151-175	0	2		2	.68
176-200	0	2		2	.68
201-225	0	1		1	.33
226-250	0	0		0	.00
251-275	0	0		0	.00
276-300	0	1		1	.33
Total	145	129	20	294	100.06

14. It has been shown that the intensity of infection in Sandy Hook puffers reaches a peak in July and sharply drops off in August.
  15. It has also been found that the number of parasites increases rapidly with size and age of the fish.
  16. Conversely, young and sexually immature puffers are particularly free of parasites.
  17. Female puffers are more susceptible than males to the metazoan parasites. Since the heaviest infestation occurred in June and July, it is assumed that this may be attributed to their more intensive feeding preparatory to spawning.
  18. There is no evidence to indicate that a heavy infestation of any one species of parasite confers resistance to the host against other species. It has been shown that about 45% of the catch was simultaneously infested with *Pseudochondracanthus*, *Lintonium* and *Bianium* and that this 45% harbored 84% of these parasites.
  19. About 63% of the puffers were infested with 1-25 parasites. All puffers harboring more than 100 parasites were females. About 11% of the fish were free of parasites.
  20. It is suggested, as a preventative measure, that young puffers (measuring up to 12 cm.) or those collected late in the season (September) be used for exhibition purpose since such fish are comparatively free of detrimental parasites which may spread to other and more important fishes.
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## 2.

The Genetics of Melanoma in Fishes. VI.  
Mendelian Segregation of Melanophore Reaction Types  
In Embryos of a Melanomatous Mother.<sup>1</sup>

MYRON GORDON<sup>2</sup> & FRED FLATHMAN<sup>3</sup>

(Text-figures 1-3).

The experimental production of melanomas in hybrid fishes, by genetic methods alone, was first discovered, not by geneticists nor oncologists, but by aquarists in 1912 and 1913. The early history of their discoveries has been pieced together by noting the details presented in the minutes of their aquarium society meetings. In their early efforts to develop new and more colorful varieties of fishes for their home aquaria these fish-breeders crossed the black-spotted platyfish, *Platypoecilus maculatus*, with the swordtail, *Xiphophorus hellerii*. The aquarists were successful in breeding strikingly beautiful hybrids but the black-spotted ones developed melanotic tumors. The fish hybridizers have continued making new combinations. One of the more recent developments has been the black-banded hybrid with either yellow or bright red back, popularly spoken of as the "tuxedo swordtail." The junior author bred some of these in his private aquarium; the mating record is given in the diagrams. One of the hybrids that developed a melanoma was turned over to the senior author for further study.

THE MELANOMATOUS FEMALE AND  
ITS BROOD.

When the black-banded, yellow-backed female swordtail hybrid was about 20 months old and 65 mm. long, it developed a melanoma measuring 12 mm. × 7 mm. × 4 mm. on her left side. A smaller tumor appeared on the other side. At the time of its death it was gravid and when it was dissected, 40 embryos were found. Their age is estimated to be about 25 days, assuming that the average gestation period is thirty days.

<sup>1</sup> The authors wish to express their thanks to the Department of Birds of the American Museum of Natural History for the use of their laboratories in the Whitney Wing where genetic and correlated studies of fishes are being continued.

<sup>2</sup> Research Associate in Genetics, New York Zoological Society.

<sup>3</sup> Private Aquarist, Woodhaven, Long Island, New York.

Under a binocular microscope, the embryos were sorted out into four genetic classes, as follows:

10, *St N*, gray-backed and well developed black bands.

9, *st N*, light colored backs and poorly developed black bands.

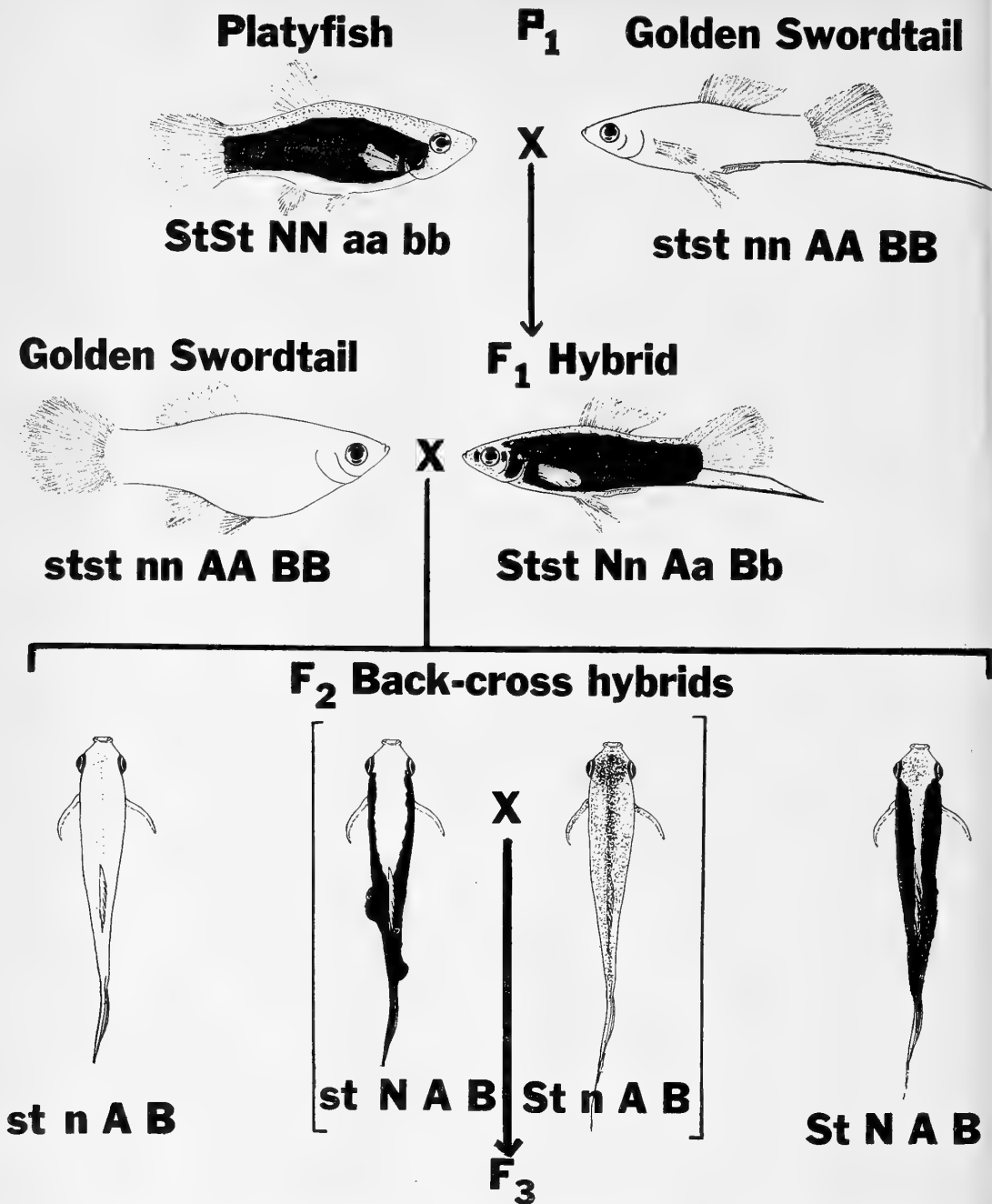
12, *St n*, completely gray, like the wild type of swordtail.

9, *st n*, extremely light in color over all.

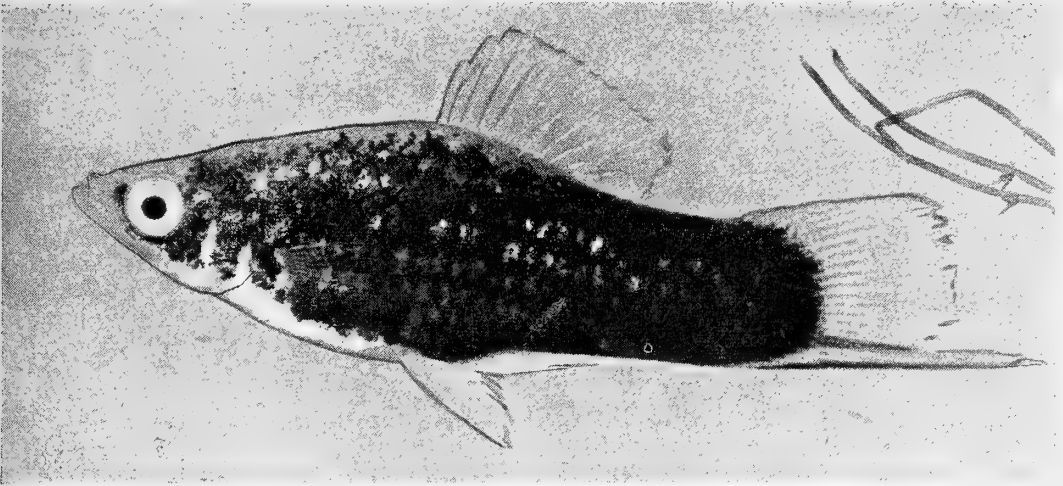
This typical backcross ratio of 1:1:1:1 was expected on the basis of two independent factors: *N* for the black band, and *St* for many tiny black pigment cells which make the fish appear gray. Bellamy (1928) showed that the black-banded pattern of the platyfish may be referred to a sex-linked dominant gene, *N*, for "nigra." Gordon (1931) confirmed this and added that *St* was a dominant autosomal factor for many small melanophores, micromelanophores, which have a "stippling" effect. When a fish has both dominant factors, *St N* it is black-banded and gray-backed. When the fish is recessive for the stippling factor, *st N*, it is black-banded and gold-backed. The black band is composed of many large melanophores, macromelanophores, while the stipple pattern is made of micromelanophores. The smaller are not the young stages of the larger but are independently developed.

THE EARLY DEVELOPMENT OF THE  
BLACK BAND.

It is significant that the four phenotypic categories, *St N*, *st N*, *St n*, *st n*, can be distinguished in hybrid fishes in embryonic stages. Gordon (1931) pointed out in his study of the development of genetic patterns in the platyfish that in pure species, the black-banded type, *N*, could not be distinguished until the birth of the fish and even at this comparatively late stage, the *N* pattern is represented by only one or two discrete macromelanophores. It is therefore

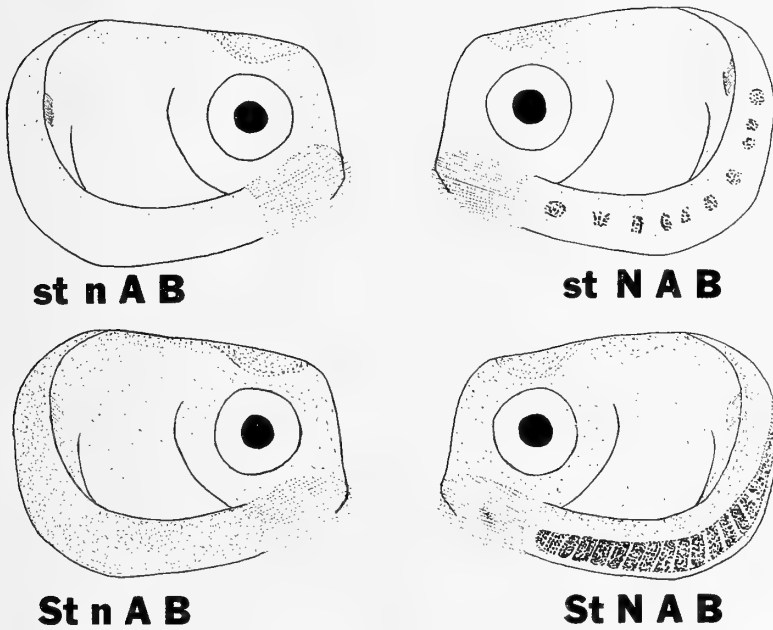


Text-fig. 1. The genetic history of the four types of embryos. A black-banded, gray-backed platyfish female, *StSt NN aa bb*, was mated to a golden swordtail male, *stst nn AA BB*. These are shown on the top. One of their black-banded, gray-backed sons, *Stst Nn Aa Bb*, was mated to a golden swordtail female, *stst nn AA BB*; the second mating is shown on the second line. The offspring of the second mating were of four types: *st n A B*, golden; *st N A B*, black-banded, golden-backed; *St n A B*, gray; and *St N A B*, black-banded, gray-backed. The four types are shown on the third row and the figures represent dorsal views of the adults. The mother of the embryos (shown in another Text-figure) is the black-banded, golden-backed type, *st N A B*; the father is the gray-type, *St n A B*. The father and mother are shown within the brackets in row three. The offspring of this mating may be seen in Text-fig. 3 on the opposite page.



Text-fig. 2. First generation hybrid. This hybrid is the product of mating a female black-banded *Platyopocilus maculatus* and the wild-type *Xiphophorus helleri*. In Text-fig. 1 it is represented on the second row to the right, under the legend F<sub>1</sub> hybrid.

### F<sub>3</sub> 25 day old embryo hybrids



Text-fig. 3. Four genetic types of embryos. These embryos represent the offspring of the third generation. *st n A B* = golden; *st N A B* = black-banded, golden-backed; *St n A B* = gray; *St N A B* = black-banded, gray-backed. The black band is much better developed in the *St N A B* type than in the *st N A B* type, indicating an interaction of *St* and *N* genetic factors. (The authors wish to thank Mr. Jack Beckenstein for his aid in the preparation of these charts.)

quite apparent that the rate of growth of the macromelanophores is much accelerated in the hybrids. This marked increase in the rate of development is brought about by two

genetic modifiers, *A* and *B* of the swordtail. Kosswig suggested this interpretation from his study of adult black-banded neoplastic hybrids. The change of the macromelano-

phore habit of growth from the normal to the pathological has also been analyzed by Gordon in his study of the *Sp* gene which is closely related to the *N* factor: *Sp* brings about the spotted pattern in pure platyfish and macromelanophore overgrowths in platyfish-swordtail hybrids.

#### THE INFLUENCE OF THE *St* GENE UPON *N*.

The *N* gene is influenced by the micromelanophore factor *St* in addition to *A* and *B* and this effect can only be detected in the embryos. For instance, in the gold-backed, black-banded hybrid embryos, *st N*, the macromelanophores are far less numerous, and form a much weaker black band, than in the gray-backed, black-banded type *St N*. This is illustrated by the diagram.

A similar situation of interaction of factors has been described by Gordon (1928) in two varieties of the platyfish: the gold, spotted platyfish, *st Sp*, had far fewer macromelanophores than the gray, spotted type, *St Sp*. In this instance the differences persist throughout life whereas in the black-banded hybrid types mentioned above, and in black-banded pure platyfish, the adult *st N* type has as strong a black band as the *St N* type.

Another instance of factor interaction involving the melanophore ratios may be found in the two genetic phases of the *Mo* gene in hybrids. The *Mo* is characterized by the presence of many macromelanophores arranged in lateral lines; usually the body is orange-red in color. Gordon (1938) has pointed out that the *St Mo* type is outstandingly more heavily spotted with macromelanophores than the *st Mo* form; indeed, the *st Mo* has but one or two spots near the head.

In platyfish-swordtail hybrids, macromelanophores alone, *st Sp*, are able to evoke melanomas. Micromelanophores, alone, *St sp*, cannot do this. Yet micromelanophores exert a definite force in intensifying the severity of the neoplasm when these cells are present together with macromelanophores. For instance, hybrids of the constitution *St Sp* develop their tumors earlier and faster than *st Sp*. This is also true in *N* hybrids: *st N* hybrids develop melanomas but the *St N* develop them first. An insight into the changing relationships between the two types of melanophores of a melanotic hybrid may be had by comparing the melanophores in *st N* embryos and in adults. In the *st N* embryo some micromelanophores are found along the dorsal ridge of the back and extend over the meninges of the brain; the number of micromelanophores found is, of course, far less than in the *St N* embryo. In the *st N* adult, practically all the micromelanophores have been eliminated by the hypertrophic activity of the macromelanophores

in the making of the black band. It appears that as the *st N* hybrid develops, its macromelanophores usurp all the melanin-producing substances.

#### SUMMARY.

The primary genic function of *St* is the formation of thousands of micromelanophores. This clothes the platyfish or the swordtail with a grayish coat of pigment. The secondary effect of the *St* gene is to accelerate the growth-promoting forces of the macromelanophores both in normal and neoplastic stages of their development. For example, more macromelanophores appear at birth of a hybrid in a *St Sp* than in a *st Sp*; more in a *St N* than in a *st N*. More macromelanophores are developed by the adult *St Sp* than by a *st Sp* platyfish; more in the *St Mo* than in the *st Mo* swordtail derivative.

Thus the *St* gene has a dual effect: first, in the production of many micromelanophores and second, in the stimulation of the production of macromelanophores when the gene *Sp*, *N* or *Mo* is present. The growth promoting effect of *St* on *Sp*, *N* or *Mo* is limited; *st* does not have the power to shift the macromelanophore growth-pattern in pure species from the normal to the neoplastic. The neoplastic activity of the *Sp* or *N* gene in hybrid fish combinations is controlled by factors *A* and *B* which are contributed by a foreign species. Perhaps at a future time, some definite physico-chemical process may be suggested in the activity of genes *St*, *A* and *B*, but at present such data are lacking.

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## 3.

Pattern and Color in the Cichlid Fish, *Aequidens tetramerus*.<sup>1</sup>

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(Plate I).

[This is a contribution from the Forty-third or Venezuelan Expedition of the Department of Tropical Research of the New York Zoological Society made under the direction of Dr. William Beebe. The expedition was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

As a preliminary to the study of some Venezuelan fishes and especially their reactions to the dry and the wet seasons, I wish to present a comparison of the pattern and color descriptions of one species of cichlid taken from ichthyological literature, with the twenty-four hour variation of a single individual of the same species.

This fish is *Aequidens tetramerus*, originally described by Heckel (*Acara tetramerus*, Heckel, 1841, *Ann. Wiener Mus.*, II, 341). It has a wide distribution, from Venezuela and the Guianas, on throughout the Amazonian drainage system to eastern Ecuador, and south to Brazil and Paraguay.

#### EIGHT DESCRIPTIONS SELECTED FROM LITERATURE.

"Color in alcohol, at the present time: in general chocolate brown; toward the back of the head almost black, lighter toward the breast; each scale with a light spot at its base. A black spot below the eye; the lateral spot below the 9-11th scales of the lateral lines, and the tail spot encircled by bright white dots which also appear farther below on the base of the fin. The soft portion of the vertical fins has several diagonal rows of black dots.

"Color in life: upper half dark greenish-brown becoming blue-gray below and violet toward the throat; sides of the head dark gray-brown, yellow-brown below; each scale, especially on the lower half of the body,

lighter in the center than the ground color; the three lateral spots black and the spots surrounding the tail spot pure white. The spinous dorsal same color as the back; the soft rays and the caudal fin brownish-yellow; the two last as well as the end of the anal fin dark greenish-brown, the pectorals brownish-yellow. The iris dark brown-yellow, lighter below with some brown shading." (Translated from the German of Heckel: *Wiener Museum D. Naturgeschichte Annalen*, 1841, Vol. 2, p. 342).

"*Coleur de l'animal conservé dans la liqueur, d'un brun chocolat avec une tache ocellée sur la dos à la base de la nageoire dorsale; le ventre paraît avoir été plus clair et les opercules dorés.*" The plate figure differs considerably from this description, showing the iris bright yellow, body in general dark greenish-brown with an elongate ocellus on the upper part of the end of the peduncle. (Castelnau, 1855, *Anim. Amer. Sud. Poiss.*, p. 15, pl. VI).

"Brown, with a black spot on the middle of the sides and with a black ocellus edged with whitish superiorly at the root of the caudal fin, the two spots sometimes united by a band; a dark spot below the orbit; a whitish streak between the eye and the nostril." (Günther, 1862, *Cat. Fishes Br. Mus.*, IV, p. 277).

"Color brown, several darker cross shades across the dorsal region; a large, black ocellus on lateral line. No other spots. Fins dusky. Lower lip yellow." (Cope, 1870, *Proc. Amer. Phil. Soc.*, XI, 570).

"Olive, with jointed, unpaired fins yellow. A large black spot before middle of side on lateral line, a vertical shade at base of caudal. As compared with *A. dimeras*, its closest ally, this fish differs in . . . lack of cross-bars." The figure shows no markings at all, except lateral spot. (Cope, 1871, *Proc. Acad. Nat. Sci. Phila.*, XXIII, 255, pl. XI, fig. 4).

"Olivâtre avec une tache noire sur le côté et une autre bordée de blanc en haute de l'origine de la caudale; ces taches parfois

<sup>1</sup> Contribution No. 651, Department of Tropical Research, New York Zoological Society.

réunies par une ligne foncée. Un point noir sous l'orbite et une ligne clair entre la narine et l'oeil. Nageoires impaires habituellement ponctuées." (Pellegrin, 1903, *Mem. Soc. Zool. France*, XVI, 171).

"Olivaceous, with 5 dark cross-bars, the first crossing the anterior 7 or 8 scales of the lateral line, the second the 9th or 10th, and 3 succeeding scales of the lateral line, below which it bears a thickish blotch; a dark spot below the posterior part of eye; a dark ocellated spot on the upper part of the base of caudal; usually a dark longitudinal band from lateral blotch to caudal spot, sometimes continued forward to the eye; vertical fins dusky, usually spotted." (Regan, 1905, *Ann. Mag. Nat. Hist.*, (7) XV, 332).

"The pond specimens deeply colored. They show faintly the vertical color bands and a lateral line from the eye to the caudal basis. This interrupted by the lateral spot. Color notes made in the field on the Puerto Bermudez specimens, show the dorsal half of the body deep blue, shading to gray ventrally. Ocellated spot on the peduncle, bordered with yellow; irregular blue-black markings on the caudal fin; fins washed with yellow; five or six longitudinal stripes of yellow on the head from the snout to the eye and cheek. In alcohol a longitudinal color band can be seen in many." (Eigenmann & Allen, 1942, *Fishes of Western South America*, p. 392).

#### COMMENTS ON AQUARIUM SPECIMENS.

This fish is fairly well known to aquarists and we find descriptions such as the following:

"Color changing; upper half green to greenish brown, bluish gray to reddish beneath, throat violet; sides with about six cross-bars, one of which intensified into a spot below the lateral line; sometimes a dark band from eye to an ocellated spot at the base of the upper caudal rays. Vertical fins spotted or barred; dorsal in its spinal part and anal dark greenish brown; soft dorsal and caudal yellowish. The color markings of the body become obscure with age, those of the fins more intense." (Rachow, 1937, *Tropical Aquariumfish*, p. 111).

"Color and markings vary greatly with age and the influence of local conditions but usually it is light green to olive brown, often with a golden or brassy tone. The sides are yellow to slate and the belly is light gray with a rose tint. A black horizontal stripe extends from the eyes, through the middle of the sides, to the caudal spot on a yellow field. Three or more, light to dark brown vertical bands run through the eyes and upper section of the body, enhancing the large area behind the eyes and another under the dorsal fin. The anterior parts of the dorsal and anal fins are dark olive and

these fins as well as the caudal, are peppered with dark spots and short lines. The body markings of young specimens are quite pronounced. More mature specimens lose the body markings and those in the fins are more pronounced." (Stoye, *Tropical Fish for the Home*, p. 168).

"No one phase seems to give an adequate representation. A slight change in light produces an entirely different effect, and as we all know, the various Cichlids have a tremendous range of color pattern, due to the influences of emotion, temperature and health." (Innes, 1934, *The Aquarium*, II, p. 277).

#### COMPARISON OF THE EIGHT DESCRIPTIONS WITH THE COLOR PHASES OF A SINGLE INDIVIDUAL.

In these eight selected descriptions, extending from Heckel in 1841 to Eigenmann and Allen, 1942, we have a cross section of pattern and color as observed and recorded by these authors. We find the following relative mention of five elements of the pattern: Lateral ocellus 8 times, caudal ocellus 7, longitudinal stripe 4, vertical bands 3, sub-ocular spot 4 times.

It is interesting to compare this with the seven phases of a single individual in the accompanying plate, figure one of which is diurnal, and all the others nocturnal. Here, the proportion is, lateral ocellus 7, caudal ocellus 3, longitudinal stripe 4, vertical bands 3, and sub-ocular spot 2 times.

#### COLOR DESCRIPTION OF PLATE.

It has been possible to reproduce the accompanying plate only in black and white, so a few notes on the lost colors are necessary. There are seven figures, all drawn from the same living fish within a period of twenty-four hours. This fish was taken from an almost dried-up mud hole at the edge of the jungle at Tenth Kilometer, Caripito, Venezuela, March 21, 1942. Dep't. Tropical Research Cat. No. 30,006; standard length 75 mm.

Figure 1 shows the typical diurnal pattern and coloration. This is dark brown above and turquoise on the ventral surface. The lateral ocellus is very black. There are five or six, greenish-brown, narrow, longitudinal stripes along the body, alternating with equally narrow stripes of grass green. The opercles are densely, the sides of the body more sparsely, dotted with turquoise blue. The belly and abdomen and the first pelvic ray are solid turquoise, and the sides of the head are alternately streaked and dotted with the same color. The fins are brownish, the vertical fins faintly barred and spotted with darker. The edge of the entire dorsal fin is warm orange.

Figures 2 to 7 show various phases of the pattern as observed at night. Brown is the dominant color, the only exceptions being the black of the ocelli, and the turquoise spots, of which traces remain on the cheeks and opercles, and in all cases the blue of the pelvic ray. All other colors of the diurnal phase are absent.

#### PATTERN IN FIVE PRESERVED SPECIMENS.

Of five other specimens collected in Venezuela, two came from the dried pool at Tenth Kilometer, two from a small muddy creek known as Rio San Pablo, and one from the clear waters of Rio Caripe. In death all are almost identical, although one was killed in alcohol, two leaped out of their aquarium the first night and died slowly, and the fifth was killed after a week in captivity.

All show the heaviest, most relaxed type of pigmentation, closely approximating Figure 5 on the plate. The whole of each fish, however, is much darker, the vertical bands considerably wider and blacker, the lateral ocellus being almost buried in its particular band. As in the fifth pictured phase, there are nine vertical bands, with a consistent branching of the eighth (counting from the caudal). In two fish, the displaced nuchal band is continuous with the rest of the ninth through eye and opercle. The caudal ocellus is indicated only by a narrow vertical mark, which I call band number one. The lateral ocellus is always in the sixth band from the tail. The boundary of the lateral ocellus is clearly marked in all the fish by a circle of turquoise dots. Others can be seen scattered anteriorly over the side of the body, and many on the opercles. No hint of the blue pelvic ray is visible, in any of the preserved fish.

#### VENEZUELAN FIELD NOTES.

The only place I could observe this species under natural conditions was in the Rio Caripe before its waters were muddied by floods. In the dried jungle pools and the small San Pablo the fish were invisible until dug up with a spade or brought to the surface in a hand net. In the Caripe they were abundant, living in loose schools in the back water above riffles. As I waded about I could distinguish them from other cichlids by the conspicuous black lateral spot. This seems the only pattern element which is present under all conditions. Several times when fish escaped from the seine and rejoined their free fellows, they became at once indistinguishable, having undergone no apparent pattern changes as a result of fear or excitement.

A number of specimens were kept in a small air-supplied aquarium in the laboratory, past which several of us walked many

times a day. These showed almost no change during the hours of daylight, and even when excited by the sudden appearance of food, the lateral spot was the only dominant mark.

#### PATTERN CHANGE IN A SINGLE INDIVIDUAL.

As already mentioned, Figure 1 shows the typical diurnal pattern, as observed in undisturbed and disturbed fish in their normal haunts and in the aquarium. At night, whether in the dimmest light, or in the illumination from a powerful flashlight, the pattern came and went in bewildering combinations of the four shifting pattern elements, caudal ocellus, longitudinal stripe, vertical bands, sub-ocular spot, in intricate changes around the permanent lateral ocellus.

Extremes are shown by Figures 2 and 5. In the former, the fish for the most part is white, shading into pale brown on head and back. Figure 6 shows the two ocelli and the eye all connected by a longitudinal stripe. Figure 3 has the sub-ocular spot, and a slight discontinuity of the stripe. In Figure 7 the stripe ends at the lateral ocellus, the posterior half and the caudal ocellus having vanished. Three vertical half bands are present on the postero-inferior quarter of the body. Figure 4 has vertical bands 1, 2, 3, 4, 5 and 7 developed (counting from the caudal), with bands 6, 8 and 9, and the posterior half of the longitudinal stripe lacking. Figure 5 is a pale phase of what persists in all preserved specimens, the most intense amount of pigmentation, lacking only the narrow longitudinal stripes of the diurnal pattern and the caudal ocellus. In this phase even the iris of the eye changes its pigmentation to emphasize and complete the ninth band on the lower part of the head.

#### PATTERN OF OTHER LIVING INDIVIDUALS.

Another individual fish of the same species which I examined six times in one night, showed phases approximating Figures 4, 5 and 7, with the vertical bands always in evidence, greatly diminished in only one case. A third fish at 11 P.M. and 2 and 3 A.M. showed no trace either of caudal ocellus or longitudinal stripe.

This brief treatment is meant only to stimulate, and to emphasize the value of future observation in the field, both by day and night. The nocturnal changes in pattern and color, as I have often observed in tide-pool fish<sup>2</sup> are something to be reckoned with in our descriptions both of well known and of newly discovered species, and in explanation of ecological adaption. In the present instance I had no opportunity to obtain detailed data on specific causes, whether psychological, sensory or environmental, of

<sup>2</sup> *Book of Bays*, page 169.

these changes, but if our keys and careful descriptions dealing with pattern and color of species and sub-species are to withstand both laboratory, aquarium and field scrutiny, individual changes must be taken into account, and reduced to correct values in diagnoses.

As one last example, Eigenmann, in the description of a new species, writes "*Aequidens potaroënsis* is 'evidently very closely related to *A. tetramerus* from which it can easily be distinguished by the dark band from the eye through the angle of the opercle.'" On this diagnosis alone it appears

in the plate as Figure 5, at least on one night, when it became and quite departed from the said species within a period of ten minutes.

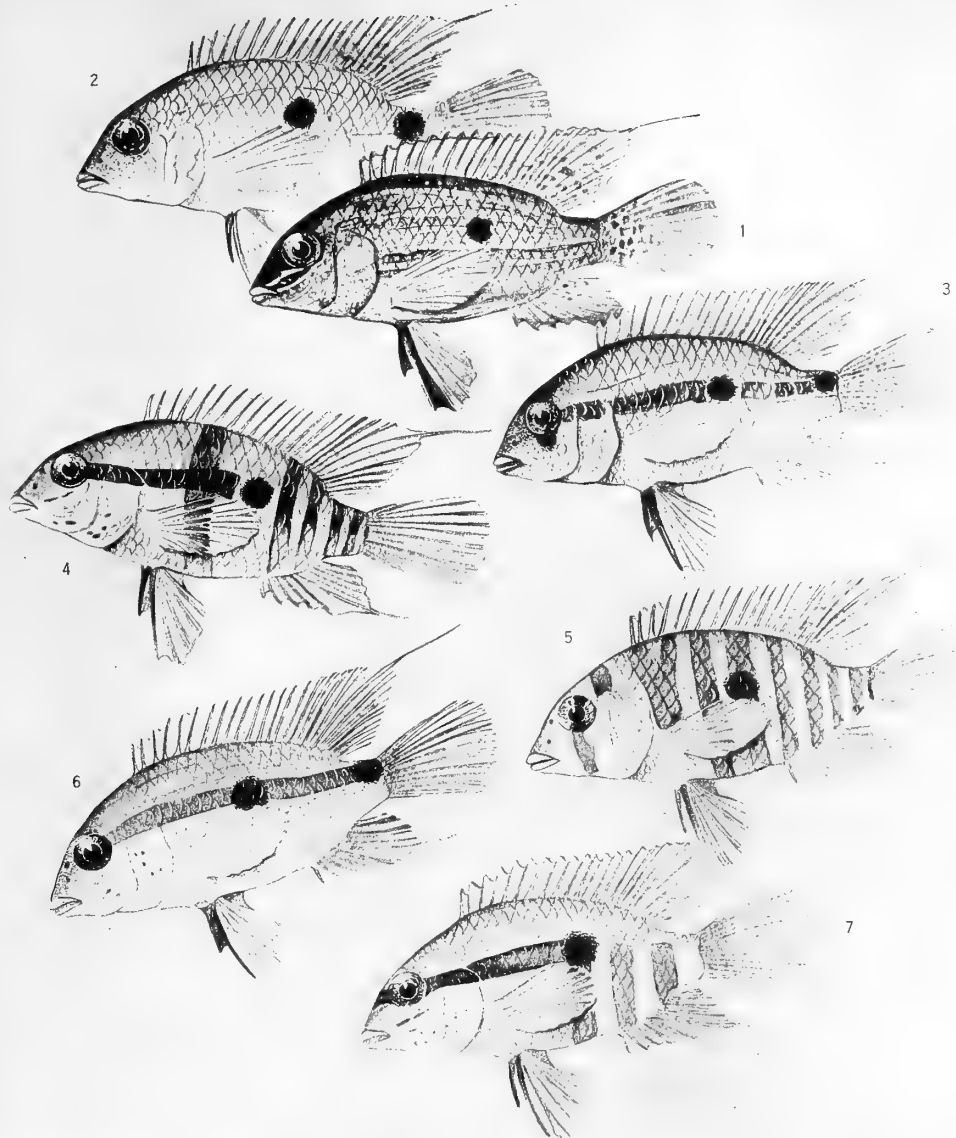
My sincere thanks go to Miss Francesca LaMonte for graciously given assistance.

## EXPLANATION OF THE PLATE.

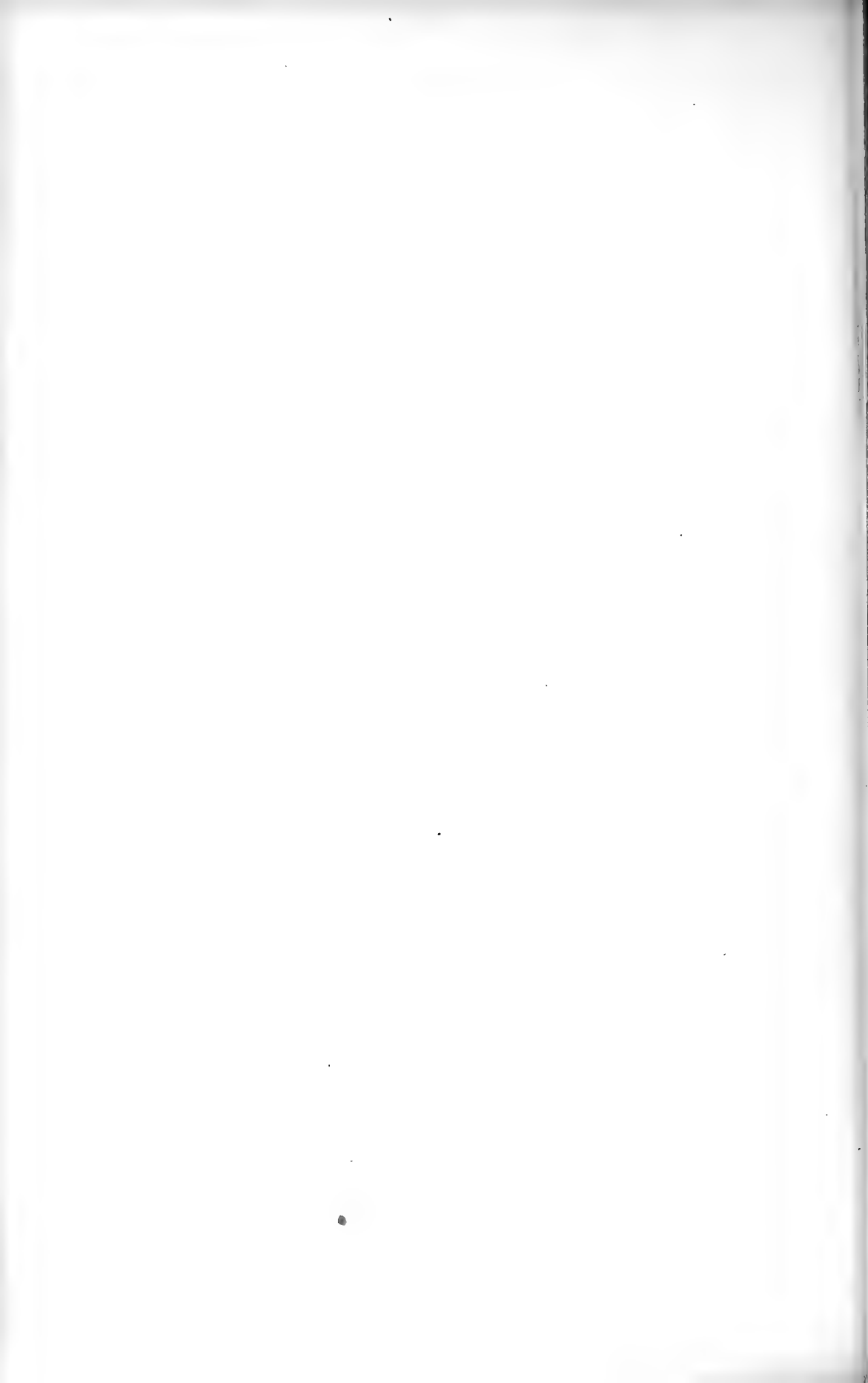
### PLATE I.

The Venezuelan Cichlid fish, *Aequidens tetramerus*. Seven pattern and color phases of a single individual fish, within twenty-four hours time. Figure 1 is the diurnal pattern, all others nocturnal. From a painting by George Swanson.

<sup>3</sup> Eigenmann, *Fishes of British Guiana*, 1912, p. 490.



PATTERN AND COLOR IN THE CICHLID FISH, AEQUIDENS TETRAMERUS.



## 4.

## A Revision of the Genera and Species of the Family Pycnonotidae (Bulbuls).

JEAN DELACOUR.

(Plates I & II; Text-figures 1-13).

The bulbuls constitute one of the most clearly defined groups of perching birds (Passeres). This means that the different genera and subgenera which belongs to the group are obviously related to one another, and rather far removed from any others. A few other genera, however, which may be fairly closely related to them, are difficult to classify in the present state of our knowledge.

In my opinion, however, bulbuls do not belong to the large Muscicapidae family group (Muscicapidae), of which thrushes and robins (Turdinae), warblers (Sylviinae), babblers (Timaliinae) and a few others are evidently members. They are too different from any of these in their general structure, proportions, feathering, behavior and habits, and there do not seem to be any definite links with them, no more than with some other very different families.

As it so commonly happens with families extending over two or more continents and numerous islands, bulbuls have been studied mostly within the artificial limits of local avifaunas, and their general grouping has been often incomplete and fragmentary, their true affinities being ignored. Major studies and lists of Pycnonotidae can be found in Sclater's *Systema Avium Aethiopicarum*, 1930; Chasen's *Handlist of Malaysian Birds*, 1935; Mathews's *Systema Avium Australasiarum*, 1930; Hachisuka's *Birds of the Philippine Islands*, 1935; Stuart Baker's *Fauna of British India Birds*, 1922-1930; Bannerman's *Birds of Tropical West Africa*, 1936; and my own *Les Oiseaux de l'Indochine Française*, 1931. All these works, however, deal only with local avifaunas.

In 1934-36, the late Baron Snouckaert van Schauburg published a distributional list of the Asiatic and East Indian Pycnonotidae, detailed but incomplete, and very uncritical. Dr. H. Oberholser in 1900 (*Trans. U. S. Nat. Museum*, XXI, p. 30, and XXII, p. 15), and in 1903 (*Smithsonian Misc. Coll.*, XLVIII, 1903, p. 155) studied different groups of African bulbuls and some Indian and Moluc-

can forms, describing a number of new genera, only a few of which can be recognized.

Finally, one must mention a study of the so-called Timaliine birds of Madagascar by Finn Salomonsen (*Ann. & Mag. N.H.*, Ser. 10, Vol. XIV, p. 60, 1934) where a number of forms are included which, in my opinion, belong to the Pycnonotidae.

The classification proposed below is more or less at variance with that adopted in these various works.

Without attempting a complete review of all the different subspecies and their local distribution, I thought it might be useful to endeavor to draw a better picture of the different genera, subgenera and species included in the Pycnonotidae as I understand them. The following conclusions are based on the examination of the large and excellent collection deposited at the American Museum of Natural History. I have been greatly helped by the work of Drs. E. Mayr and James Chapin in rearranging them.

In the field, I have had a good deal of experience with the Asiatic, Malay and Madagascan species, and also with some of the African ones. The observation of these birds in life and the study of their general behavior has given me a better understanding of their characteristics. This has been supplemented by the study of many live forms in captivity in my former collections and in others, public and private.

Bulbuls are of moderate size, varying from that of an English sparrow to about that of an American robin. They have rather short wings and a comparatively long tail; their beak is never large, but is slender to moderately thick, notched, with rictal bristles usually well developed; nostrils are long or oval, more or less operculated. Their legs and feet are always rather weak, usually small and often very short.

The following characteristics are peculiar to the Pycnonotidae: the body feathers are long, soft and fluffy, particularly on the lower back. The skin is thin and the neck is

very short and more or less devoid of feathers behind, so that a bulbul with an outstretched neck shows a somewhat bare patch between the nape and upper back feathers, a feature quite characteristic of the group. There are always some hair-like feathers on the nape, often long and conspicuous, sometimes weak and difficult to detect. This is, however, not a diagnostic family characteristic as it is also found in different other birds. Most of the bulbuls are olive-green, yellow or brown, with or without white, gray, black or yellow marks. A number have lightly colored under tail-coverts, varying from red to yellow, white or rufous, and some have bright yellow or scarlet spots or streaks on the head, and conspicuous ear-coverts. Many bulbuls are crested, but the presence or the absence of a crest and its relative length and shape is of little importance. Frequently this does not constitute even a specific character, since in several cases some subspecies of the same species are crested while others are not. Several groups have also lengthened, shiny and ornamental throat feathers, white, yellow or reddish-copper color. Others have long upper tail-coverts and lengthened feathers on the rump and lower back, ornamented with spots and marks.

In all bulbuls both sexes are alike in plumage and often also in size, but in a few cases the male is much larger than the female. Immatures are not spotted and differ but little from the adults. In these points, they widely differ from the flycatchers, thrushes and robins. Many live in forests and their edges, others in sparsely wooded or bushy surroundings and quite a number frequent cultivation and gardens. They are noisy, their notes being always short and loud, either melodious or harsh according to genera and species. Many can be considered good songsters. They generally live in groups, outside of the breeding season, some species in large flocks, and they mix with other birds in wandering hunting parties.

Most bulbuls are fruit and berry eaters, to which they add insects, while a few are mainly insectivorous. The latter are found among the strong or compressed bill forms.

The majority of species are sedentary, but some migrate, the northern breeders in Asia to a great extent; they are the longer-winged forms, particularly *Microscelis*. All bulbuls build cup-shaped nests and lay heavily marked eggs.

Representatives of the Pycnonotidae, as defined above, are found all over Africa, in Madagascar and the Mascarene Islands, Asia, the Philippines, the Malay Archipelago and the Moluccas.

Of thirteen genera, eight are confined to Africa (*Calyptocichla*, *Boeopogon*, *Ixonotus*, *Thescelocichla*, *Chlorocichla*, *Phyllastrephus*,

*Bleda*, *Nicator*), three to Indo-Malaya (*Spizixos*, *Setornis*, *Microscelis*), while two (*Pycnonotus* and *Criniger*) are found in both regions. In Madagascar one finds species of the African genus *Phyllastrephus* and a form of the species *Microscelis madagascariensis*, which is represented in the Mascarene Islands and from India to China and Indo-China.

A few isolated and puzzling genera have a much discussed and still uncertain position:

The curious *Hapalopteron familiare* from the Bonin Islands, usually considered a bulbul, is so far removed in proportions and plumage pattern that it is better rejected from the group. It may be an aberrant *Zosterops*.

*Tylas eduardi* from Madagascar, also usually considered a bulbul, does not fit in well, widely differing in the proportions of the wings and tail, the shape of bill, the pattern and color of its plumage. In habits it is also peculiar, living in tree tops of forests and being slow in movements, reminding one somewhat of the Asiatic *Cochoa*. It is purely insectivorous and may be a true Turdine bird.

The African *Hypergerus atriceps* has feathers somewhat recalling those of the Pycnonotidae, but its long, decurved beak, its high legs and its ground habits make it unlikely to be a true bulbul.

The proportions and color pattern of another African bird, *Neolestes torquatus*, make it difficult to accept it in the present group, although it has some characteristics suggesting affinities and is certainly not a shrike. It may be a very aberrant *Pycnonotus*.

Only detailed studies of the anatomy, habits and behavior of these four peculiar birds can decide whether or not they can be included in the Pycnonotidae. Until this is accomplished it is best not to consider them as true bulbuls. They are not discussed any further in this paper.

Several other genera have been assigned by different authors to the Pycnonotidae. Such are, on one side, the fairy bluebirds (*Irena*) and on the other the leaf birds and ioras (*Chloropsis*, *Aethorhynchus* and *Aegithina*). They all differ greatly from the true bulbuls in plumage texture, pattern and colors, while males, females and young are conspicuously unlike. The proportion of the tail and wings, their legs and feet, are also very different. They are better considered as forming separate families, possibly not very far from the Oriolidae. But this still remains an open question.

On the other hand, I have included with the Pycnonotidae several Madagascan birds classed in the Timaliidae by many authors under the generic names of *Bernieria*, *Crossleyia*, *Xanthomixis* and *Oxylabes*. In fact,

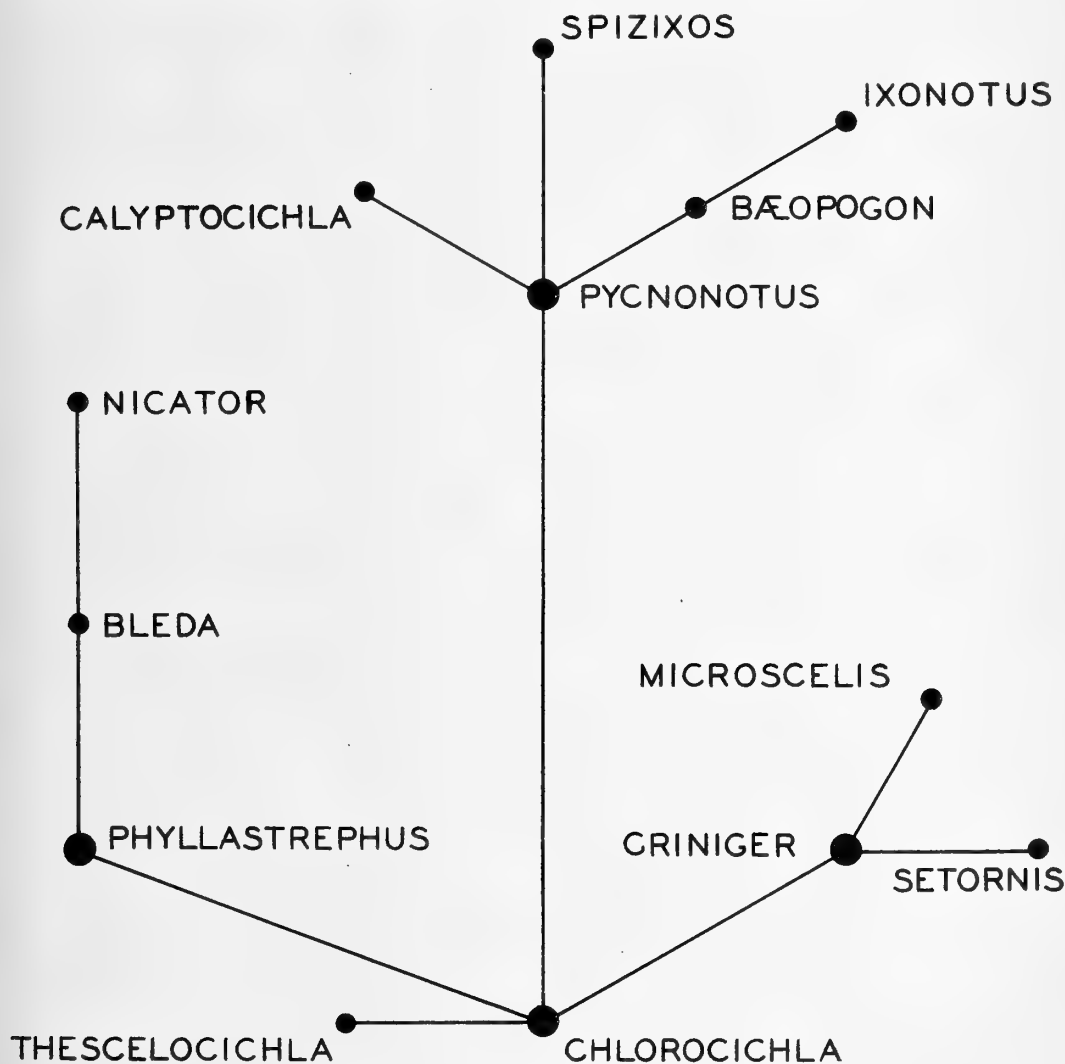


they cannot be separated from the African *Phyllastrephus* in which I place them. "*Bernieria*" *madagascariensis* and "*B.*" *zosterops* are evidently quite close to such species as *Phyllastrephus icterinus* and *P. xavieri*; all of them show an extraordinary difference in the size of males and females, a very peculiar feature. The so-called "*Oxylabes*" *tenebrosa*, *xanthophrys* and *cinereiceps*, although aberrant, rare and restricted in distribution, are certainly nearer to *Phyllastrephus* than to *Oxylabes madagascariensis*, a true Timaliine bird, completely different in proportions, shape and color pattern, with a much thicker bill and shorter wings, as is also *Mystacornis crossleyi*, both of which live on or near the ground. Close resemblance between Madagascan *Bernieria* and African *Phyllastrephus* has been long ago pointed out, particu-

larly by Hartlaub (Vog. Madag., 1877, p. 144), by Milne-Edwards and Grandidier (Hist. Phys. Madagascar, Vol. XII, p. 348) and more recently by J. Chapin. That it has escaped others shows once more the danger of the separate study of local avifaunas.

The bulbuls, that is to say, the species which show the general characteristics which I have mentioned above, can in my opinion be divided into thirteen genera, a very much smaller number, of course, than is usually accepted<sup>1</sup>, and some can conveniently be subdivided into subgenera. Their relationships are more or less close

<sup>1</sup> Sclater (Systema Avium Aethiopicarum) recognizes 24 genera (including *Bernieria* and allies, and *Nicator*, not classified by him as Pycnonotidae), while Snouckaert (Orgaan Nederl. Vogelk.) recognizes 21 for Asia and Malaysia (not including *Chloropsis*, *Aethorhynchus* and *Aegithina*, leaving out—work not completed—many species of the *Criniger-Microscelis* group).



Text-fig. 1. Relationship of the bulbuls.

and of four principal groups, the three more specialized ones can be linked to a central and more generalized one (see Text-fig. 1). The species are reduced to 109, an average of 8.4 per genus, but five of the latter remain monotypic, while one includes 47, another 23.

In defining these genera, an ensemble of characters of real importance has been considered. Others have been disregarded. As I have said above, the presence or absence of a crest is a negligible feature as it varies within the same species (*Pycnonotus leucotis* and *P. dispar*, for instance). Most important are the general pattern and color of the plumage, the shape of the bill and nostrils, the length of the tarsus and toes. A few species show slight serrations near the tip of the upper mandible, close to the terminal notch and this has been considered important enough to separate them generically. That it has no great significance is shown by the fact that such otherwise closely allied species as *virens* and *mazukuensis*, the first of which has serrations and the second none, would have to be placed in two allegedly different genera, *Andropadus* and *Arizelocichla*, which then become ridiculously heterogeneous; also one is at a loss to know where to put other forms with a certain roughening of the edge of the upper mandible, which cannot be called serration. The general shape of the rectrices also is of value, but not their relative length, as more or less graduated or forked tails are found in subspecies of the same species (*Pycnonotus flavescens* and *Microscelis madagascariensis*, for example). Life habits, voice, behavior, nesting and eggs all have to be taken into consideration and have as great a value as morphological characters.

The least specialized group among the Pycnonotidae is the African genus *Chlorocichla*, with moderately long, strong bill and legs, rather long wings and tail, colors varying from brown to bright olive-yellow, and a white or yellow throat patch. They are evidently linked to the short-billed *Pycnonotus* and allies (*Spizixos*, *Calyptocichla*, *Boeopogon*, *Ixonotus*) through the larger *Andropadus*; to the *Criniger* group (including *Setornis* and *Microscelis*) and to *Thescelocichla*, and also to the straight-billed, long-legged *Phyllastrephus*, *Bleda*, and *Nicator*. The *Pycnonotus* group does not appear to have any near allies on its more specialized end, neither has the *Criniger-Microscelis* group, if, as I have said before, one does not believe in their close relationship with *Irena*, *Chloropsis*, *Aethorhynchus* and *Aegithina*. On the contrary the *Phyllastrephus-Bleda-Nicator* group, less specialized, with stronger legs and longer beak, has some resemblances to some Timaline birds on one side, and to certain hooked-

billed groups such as *Campephagidae*, *Pri-onopidae*, *Vangidae* and certain African genera so far included in the *Laniidae*.

#### A. *Pycnonotus* GROUP.

This first group of bulbuls is composed of numerous species, the greatest number of which cannot be generically separated and form the genus *Pycnonotus*, while a few are different enough to be retained as forming small distinct genera.

They all have a comparatively short bill; the culmen is curved and not sharply ridged, the gonyes almost straight, nostrils oval or elongated, operculate to different degrees. Rictal bristles rather weak. Tarsus short or moderate. Wings rather short, about equal to the tail, which is comparatively long, square, rounded or slightly graduated. It is in this group that the plumage is most varied or vividly marked, ranging from black to olive-green, yellow, white, gray, brown, sometimes brightened by red and yellow spots and patches on the head, while a number have bright under tail-coverts, white, yellow or crimson.

Although completely arboreal, the greatest number of the bulbuls of this group frequent bush or park-like country; many have become accustomed to garden life and are found in cultivated areas. Some, however, are forest birds. All these bulbuls have loud short notes, quite characteristic of the group.

#### I. GENUS *Spizixos*.

Blyth, 1845. Type: *Spizixos canifrons*.

Bill short and very thick, whitish-yellow; plumage olive-green and gray. Crested or not.



Text-fig. 2. *Spizixos canifrons*.

1. *S. canifrons*: Eastern Himalaya, Burma, S. W. China, Northern Indo-China.
2. *S. semitorques*: Central and Southern China and Northern Indo-China, Formosa.

These bulbuls live at high altitudes in the south of their range among brush and near villages and on the edge of forests. They stand close to *Pycnonotus*, but their very peculiar beak and color entitles them to generic rank. *S. canifrons* is crested while *S. semitorques* is not.

II. GENUS *Pycnonotus*.

Boie, 1826. Type: *Turdus capensis*.

Bill moderately thick and long for the group; colors and pattern very variable. Feathers on the crown erectile and either elongated or normal in length.

Subgenus *Euptilosus*.

Gray, 1853. Type: *Brachypus eutilotus*.

Bill rather long and strong, rectal bristles long and black; feet dark gray or black. Wings rather long and tail graduated. General color brown above and whitish below. Long crest of rounded feathers on occiput. Rump feathers ample and very long, marked with white and dark brown. All lateral rectrices with white tips.

1. *P. eutilotus*: Malay Peninsula, Sumatra, Banka and Borneo.

2. *P. urostictus*: Philippines and Borneo.

*P. urostictus* has a fleshy bare ring round the eye, but otherwise resembles closely *P. eutilotus*; it cannot be subgenerically separated. They are birds of open ground and cultivated areas.

Subgenus *Microtarsus*.

Eyton, 1839. Type: *Microtarsus melanoleucus*.

Bill moderately long and thick, black like the legs. Wings rather long and tail graduated. General color black, marked with white on the wings. No crest. Rump feathers and upper tail-coverts very long. Lives in forest.

3. *P. melanoleucus*: Malay Peninsula, Sumatra, Siberut I. and Borneo.

Subgenus *Brachypodius*.

Blyth, 1845. Type: *Turdus melanocephalus atriceps*.

Bill, feet and legs small. General color bright olive-yellow or green, and black or gray. No crest, but feathers of crown erectile and rounded. Wings short; tail graduated. Rump feathers and upper tail-coverts very long and marked with black.

4. *P. atriceps*: Assam, E. Bengal, Burma, Andaman Islands, West and South Indo-China, Malay Peninsula, Sumatra, Java, Borneo and neighboring islands, Palawan.

Forms with gray underparts and back, instead of olive-yellow, are but color phases.

5. *P. poiocephalus*: S. India.

Forest bulbuls, keeping to high trees.

Subgenus *Rubigula*.

Blyth, 1845. Type: *Turdus dispar*.

Bill and legs rather short and weak, black or dark brown. Wings short; tail rather long, square or rounded. Upper parts bright olive-yellow, head black or gray; underparts

yellow, gray or mottled black and white. Crested or not. Iris crimson or yellow.

6. *P. dispar*: Western, Central, N. Eastern India, Burma, Yunnan, Indo-China, Siam, Malay Peninsula, Sumatra, Borneo and Java.

7. *P. melanicterus*: Ceylon.

8. *P. squamatus*: Malay Peninsula, Sumatra, Borneo, Java.

9. *P. cyaniventris*: Malay Peninsula, Sumatra, Borneo.

These are all forest birds. I consider *flaviventris* (and its local races), *montis* and *gularis* as subspecies of *dispar*; *flaviventris* is similar to *dispar* except for its pointed crest which becomes gradually shorter as it ranges south; *dispar* has a shiny red throat and *flaviventris* has usually a black one, but specimens with a red throat, as well as intermediates, are not uncommon in the southern and eastern parts of its range; *gularis* is but a small, duller form of *dispar*.

Subgenus *Otocompsa*.

Cabanis, 1851. Type: *Lanius jocosus*.

Bill moderately strong, black; legs small and black. Wings short, tail long, square or rounded. Upper parts plain brown or greenish-gray; crown black; ear-coverts forming patches; throat white; underparts whitish-brown, with or without yellow streaks; a black or brown broken collar on the upper breast, more or less definite; under tail-coverts crimson, orange yellow or yellowish-white. Crested or not. Iris brown.

10. *P. jocosus*: India, Burma, S. China, Indo-China, Siam, the Andaman and Nicobar Is., Malay Peninsula. Introduced into different other countries.

11. *P. xanthorrhous*: N. E. Burma, N. Siam, N. Indo-China, S. and C. China.

12. *P. sinensis*: E. C. and S. E. China, E., N. and C. Indo-China, Formosa, Hainan.

All these bulbuls live in open country with scattered trees, clearings around cultivation and human dwellings. They all have similar habits and voices. They are familiar garden birds, particularly *jocosus* and *s. sinensis*. Northern forms of *sinensis* only are migratory. The general pattern of coloration is alike in all species, but *jocosus* and *xanthorrhous* have no olive green in their plumage, while *sinensis* is suffused with it; *jocosus* only has a long pointed crest. That these species are closely related is furthermore shown by the following facts: there is a scarlet patch on the cheeks of *jocosus*, a smaller one at the base of the lower mandible in *xanthorrhous*, and a still smaller one at the same place in *sinensis taiwanus*; it is absent in other races of *sinensis*, including *hainanus*; *jocosus* and *taiwanus* have white ear-coverts, other races of *sinensis* brown or white, and *xanthorrhous* brown; *jocosus* has wide white tips to the rectrices, except the central pair, broader on the outside ones; *xanthorrhous* has very narrow white tips, while *sinensis* has only indistinct pale edgings.

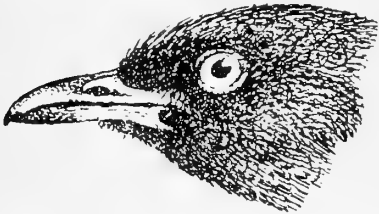
### Subgenus *Pycnonotus*.

Boie, 1826. Type: *Turdus capensis*.

Bill and legs rather strong and black. General color brown or brownish-gray, darker above, lighter below, plain or mottled, exceptionally tinged with olive (*leucogenys*); head black or brown with more or less elongated feathers on the crown forming a crest in some cases. Wings moderate; tail long and square, often tipped with white; under tail-coverts crimson, yellow or white. Ear-coverts white, brown or black. These bulbuls are larger, longer and coarser than those of the *Otocompsa* subgenus.

13. *P. capensis*: S. Africa.

14. *P. nigricans*: S. and S. W. Africa.



Text-fig. 3. *Pycnonotus barbatus tricolor*.

15. *P. barbatus*: Africa, Arabia, Palestine, Syria, Cyclades I.

16. *P. leucotis*: Mesopotamia, Persia, Baluchistan, N. W. & C. India.

17. *P. leucogenys*: Himalaya and N. W. India from Afghanistan to Assam and north of the Brahmaputra to Dihang River.

18. *P. cafer*: Ceylon, India, Burma, S. China, Siam, Indo-China, Java.

All these typical bulbuls are birds of cultivated and open countries, like those of the *Otocompsa* group, but they are stronger, with longer wings, broader tails and a more uniform plumage.

*P. barbatus* includes all African (Ethiopia and North Africa), Arabian, Palestinian and Syrian birds, which replace one another geographically and have white under tail-coverts in the north and west, gradually changing to pale and bright yellow to the south and to the east, where they have light tips to the tail, black head and throat, thus approaching *leucotis*. On account of their very different color pattern, I consider *leucotis* and *leucogenys* two different species.

*P. cafer* includes all the Asiatic forms with a white rump, almost black with crimson under tail-coverts in the west gradually changing to light gray in the east. Isolated forms in S. Siam, S. Indo-China and Java (*thais*, *germaini* and *aurigaster*) are pale, with yellow under tail-coverts, but evidently belong to the same species and have nothing whatever to do with *xanthorrhous*, which they only superficially resemble. Some birds from western Siam have orange under tail-coverts, thus providing a link.

### Subgenus *Alcurus*.

Blyth, 1843. Type: *Trichophorus striatus*.

Bill and legs dark brown, rather weak; general color olive, striped with white, or plain above, and mottled with white or yellow below; throat white or yellow. Crested or not.

19. *P. striatus*: Himalaya, Burma, Yunnan, N. Siam, N. W. Indo-China.

20. *P. leucogrammicus*: Sumatra.

21. *P. tympanistrigus*: Sumatra.

These three species are certainly related, the first two rather closely, having both a striated plumage above and a full crest. But the sharp differences in the size and in the shape and length of the elongated feathers of the crown are sufficient to make me consider them as two separate species. *P. tympanistrigus*, a rare species, is more distantly related but all the same certainly not very far from *leucogrammicus*, which it much resembles in size and in color, with the exception of the crown and upper back. All three frequent forests and scrub at high altitudes.

### Subgenus *Hemitarsus*.

Bonaparte, 1850. Type: *Turdus ochrocephalus*=*zeylanicus*.

Largest sized species of the genus; bill and legs rather short, but strong; crown with short, stiff, decomposed yellow feathers; upper parts olive brown and lined with white.



Text-fig. 4. *Pycnonotus zeylanicus*.

22. *P. zeylanicus*: Malay Peninsula, Sumatra, Nias I., Borneo, Java.

An open country, lowland bird. Its particularly large size and the peculiar feathers of its crown do not seem, however, to warrant generic differentiation, the bird being a true *Pycnonotus* in every other way. In spite of the tremendous difference in size, it resembles closely, *P. tympanistrigus* in shape and color.

### Subgenus *Loidorusa*.

Cabanis, 1851. Type: *Muscicapa goiavier*.

Short-winged bulbuls, with rounded or slightly graduated tail, weak or moderate bill and feet, black or brown. General color olive gray or brown, many species with a green wash on the upper parts and the edge of wing and tail feathers; bend of wing yellow or whitish. Less differentiated forms almost plain brown, more differentiated ones with white or yellow supercilium or other bright marks on the face and yel-

low under tail-coverts. Feathers of the crown sometimes elongated, but no pointed crest.

23. *P. bimaculatus*: Sumatra, Java, Bali.
24. *P. finlaysoni*: Burma, Yunnan, Siam, Indo-China, Malay Peninsula.
25. *P. xantholoemus*: S. India.
26. *P. penicillatus*: Ceylon.
27. *P. flavescens*: Assam, Burma, Siam, S. Yunnan, Indo-China, Borneo.
28. *P. goiavier*: S. Siam, S. Indo-China, Malay Peninsula, Sumatra and neighboring islands, Java, Bali, Borneo, Philippine Is.
29. *P. luteolus*: Peninsular India and Ceylon.
30. *P. plumosus*: Malay Peninsula, Sumatra and neighboring islands, Java, Borneo, Palawan, Calamianes, Cagayan, Sulu.
31. *P. blanfordi*: Burma, S. Indo-China, Siam, N. Malay Peninsula.
32. *P. simplex*: Malay Peninsula, Sumatra and neighboring islands, Borneo, Java.
33. *P. brunneus*: Malay Peninsula, Sumatra and neighboring islands, Borneo.
34. *P. erythrophthalmos*: Malay Peninsula, Sumatra and neighboring islands, Borneo.

The members of this large group of bulbuls are certainly much more closely related among themselves than any others, and one leads fairly well to the other, as arranged above. They are all birds of forest undergrowth and scrub, some, particularly *goiavier*, becoming familiar garden birds. *Leucops*, from Borneo, is evidently a subspecies of *flavescens* from which it hardly differs; the slightly graduated tail of the latter does not entitle it to generic distinction, as often accepted (*Xanthixus*). In fact, it is the northern or mountain representative of *goiavier*, as *luteolus* is its western counterpart. The separation of *penicillata* in the genus *Kelaartia* also seems unnecessary, although it is a very well-marked species; but its face ornaments are only an over development of those found in neighboring forms. *P. xantholoemus* is a rare and peculiar bird, but seems to be an unstreaked, grayer and paler representative in the west of *P. finlaysoni*.

### Subgenus *Andropadus*.

Swainson, 1831. Type: *Turdus importunus*.

Bill small or moderate, black or horn brown, with or without small serrations before the terminal notch on the upper mandible. Legs and feet moderate in size and variable in color like the bill. Wings and tail moderately long; general color uniform olive brown or green, lighter below, sometimes gray or yellow with a black or gray head; one with yellow malar patches. Not crested.

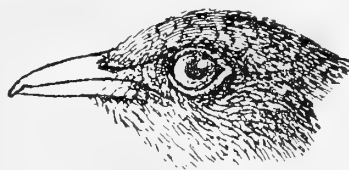
35. *P. masukuensis*: East Africa (highlands).
36. *P. virens*: West Africa to Kenya and Nyasaland.
37. *P. gracilis*: West Africa to Uganda and Kenya.
38. *P. curvirostris*: Liberia to Uganda, Congo and Angola; Fernando Po.
39. *P. importunus*: South Africa.
40. *P. insularis*: East Africa (coast).
41. *P. latirostris*: West Africa to Uganda and Kenya.
42. *P. gracilirostris*: West Africa to Angola, Uganda, Kenya.
43. *P. nigriceps*: Kenya, Tanganyika and Nyasaland.
44. *P. montanus*: Cameroon.
45. *P. tephroloemus*: Cameroon, Uganda and Tanganyika.
46. *P. milajansis*: Kenya, Tanganyika, Nyasaland, E. Rhodesia.
47. *P. chlorigula*: Tanganyika.

Several generic names proposed by Oberholser cannot be recognized on account of the confusion or lack of importance of the characters invoked, and the following are synonyms of *Andropadus*: *Eurillas*, *Stelgedillas*, *Stelgido-cichla*, *Charatillas*, *Arizelocichla*. Bulbuls of this large African subgenus are shy forest birds of somber plumage and several bear close resemblance to the Indo-Malayan *Loidorusa*. *P. tephroloemus* and *P. milajansis*, for example, show the same pale shaft stripes on the ear-coverts as *P. plumosus*. Bill and legs vary much in length and strength throughout the subgenus, as in the previous ones. These variations are not linked with the presence or absence of serrations or roughening on the upper mandible, nor to the color or pattern of the plumage.

### III. GENUS *Calyptocichla*.

Oberholser, 1905. *Criniger serinus*.

The African species *C. serina* is undoubtedly closely related to the subgenus *Andropadus*, but it differs considerably from all *Pycnonotus* by its almost straight and slender bill, which is narrow, higher than broad and flesh colored; operculum completely feathered. Plumage light olive above, bright yellow below. Tail rather short and wings long. A forest species.



Text-fig. 5. *Calyptocichla serina*.

1. *C. serina*: West Africa (Sierra Leone to the Congo); Fernando Po.

IV. GENUS *Boeopogon*.

Heine, 1860. Type *Criniger indicator*.

Not far from *Andropadus*, but has the bill short and broad, wider than high at the base, nostrils operculate and half covered by front feathers. Bill and legs black or gray. Rictal bristles weak. Tail short. ( $=\frac{3}{4}$  wing), the two median pairs of rectrices greenish black, the others whitish-yellow. Upper parts olive green; under parts paler; throat gray. Forest bird of the tree tops.

1. *B. indicator*: West Africa to Uganda and Angola.

I think Stresemann is right in considering *B. clamans* as a color phase of *B. indicator*, and not as a separate species.

V. GENUS *Ixonotus*.

Verreaux, 1851. Type: *Ixonotus guttatus*.

Resembles *Boeopogon* in having the outer pairs of rectrices yellowish-white. Bill longer and narrower. Very peculiar plumage pattern, olive gray above with large white spots on the wing and lower back, yellowish-white below. A bird of the tree-tops, more active than *Boeopogon*.

1. *I. notatus*: Liberia to Angola, the Congo and Uganda.

B. *Chlorocichla* GROUP.VI. GENUS *Chlorocichla*.

Sharpe, 1881. Type: *Trichophorus flaviventris*.

Bill black, moderately long and thick, slightly compressed; nostrils oblong with operculum slightly feathered; culmen and gonys gently curved; culmen notched at the tip. Nuchal hair short; rictal bristles moderately developed. Tail equal to wing, rounded or slightly graduated. Feet strong, legs rather long, gray. General color brown to olive yellow above, paler below, the throat forming a white or yellow patch, more or less clearly defined. These bulbuls live in forest thickets.



Text-fig. 6. *Chlorocichla falkensteini falkensteini*.

1. *C. falkensteini*: Cameroon and Angola.
2. *C. simplex*: West Africa, from Portuguese Guinea to N. Angola, east to Ituri and Semliki.

3. *C. flavicollis*: West Africa to Bahr-el-Ghazal, Uganda, and Lake Tanganyika.

4. *C. flaviventris*: East and South Africa.

5. *C. loetissima*: Belgian Congo, Uganda and Kenya.

The five species of *Chlorocichla* have been scattered by different authors over many genera. Others have associated them with *Pyrrhurus scandens*, which I consider a *Phyllastrephus*, having a straight compressed bill. These five species are much alike in shape, proportions and color pattern, but as a group they are altogether allied to *Pycnonotus*, *Crimiger* and *Phyllastrephus*, between which they constitute a link.

VII. GENUS *Thescelocichla*.

Oberholser, 1905. Type: *Phyllastrephus leucopleurus*.

Bill like *Chlorocichla*; feet and legs strong. Tail long and graduated, fan-shaped, the four lateral pairs of rectrices with large white tips. Color pattern peculiar, olive brown above, the face and breast gray streaked with white, the remaining under parts white tinged with yellow. Habits also peculiar; a bird of the raphia swamps.



Text-fig. 7. *Thescelocichla leucopleura*.

1. *T. leucopleura*: West Africa.

C. *Phyllastrephus* GROUP.VIII. GENUS *Phyllastrephus*.

Swainson, 1831. Type: *P. terrestris*.

Bill long, slender, compressed and carinated; culmen almost straight, curved only near the tip, with a terminal notch, often strong; gonys slightly convex. Nostrils slit-shaped set in a depression; rictal bristles variable. Legs longer than bill; feet strong. General color pale brown, olive green or yellow, lighter and sometimes brighter below; a few have the head gray, the throat white; wings and tail often reddish-brown. Tail rounded or graduated. Sexes different in size; in some cases the male is strikingly larger than the female and has a much longer bill. The bulbuls of this genus are forest birds, some living near the ground, in thickets and the lower vegetation; they are mainly insectivorous, and the nearest of the family to Timaliine and Sylviine birds.

1. *P. scandens*: West Africa, east to Bahr-el-Ghazal.

Text-fig. 8. *Phyllastrephus terrestris terrestris*.

2. *P. terrestris*<sup>2</sup>: East and South Africa.
3. *P. cerviniventris*: Kilimanjaro to Nyasaland, Katanga and N. Rhodesia.
4. *P. poensis*: Fernando Po and Mt. Cameroon.
5. *P. hypochloris*: W. Uganda and E. Congo.
6. *P. fulviventris*: Angola.
7. *P. olivaceo-griseus*: Kivu (Congo), Ankole (Uganda).
8. *P. flavostriatus*: S. E. Africa.
9. *P. rabai*:<sup>3</sup> Rabai and Shimba Hills near Mombasa, E. Africa.
10. *P. lorenzi*: Semliki and Ituri districts (B. Congo). Not examined.
11. *P. albigularis*: West Africa to Uganda.
12. *P. fischeri*: Kenya and Tanganyika.
13. *P. baumanni*: Togo and Ivory Coast.
14. *P. poliocephalus*: Mt. Cameroon.
15. *P. orostruthus*: Portuguese E. Africa. Not examined.
16. *P. cabanisi*:<sup>4</sup> Uganda, E. Belgian Congo to N. Rhodesia.
17. *P. icterinus*: West Africa to Uganda.
18. *P. xavieri*: Angola, S. Cameroon, and French Congo.
19. *P. madagascariensis*: Madagascar generally.
20. *P. zosterops*: N. and E. Madagascar.
21. *P. tenebrosa*: C. E. Madagascar.
22. *P. xanthophrys*: E. and S. E. Madagascar.
23. *P. cinereiceps*: E. and S. E. Madagascar.

I have arranged in a new way the sequence of species, but for specific grouping and names I have used those adopted by J. Chapin in yet unpublished notes. The first species are those with a thicker bill and browner coloration, the last those with a narrower and more compressed bill and yellower plumage.

<sup>2</sup> *P. strepitans* I provisionally consider a subspecies of *terrestris*, although Friedmann & Loveridge report both forms from Bagamoyo and Dar-es-Salam (Bull. C.M.Z., LXXX, p. 231).

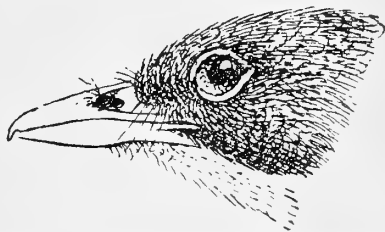
<sup>3</sup> *debilis* is probably a synonym.

<sup>4</sup> *sucosus* is probably a subspecies.

## IX. GENUS *Bleda*.

Bonaparte, 1857. Type: *Dasycephala syndactyla*.

Bill narrow and high, compressed; culmen straight and strongly hooked at the tip; gonys convex; nostrils oval; strong rictal bristles. Legs long and strong; middle and outer toes fused as far as the first joint. Olive green above, bright yellow below, wings and tail reddish or green; head gray in one species. Female much smaller than male, which has a larger bill. These birds live in the undergrowth of forests and are insectivorous.

Text-fig. 9. *Bleda syndactyla syndactyla*.

1. *B. syndactyla*: West Africa, east to Uganda.
2. *B. eximia*: West Africa, east to Uganda.
3. *B. canicapilla*: N. West Africa.

## X. GENUS *Nicator*.

Hartlaub & Finsch, 1870. Type: *Lanius chloris*.

Bill strong, compressed and hooked; thicker near the tip than in *Bleda*; gonys convex; legs and feet strong; general color olive yellow and gray, with yellow spots on the wings; tail margined with yellow below. Soft, fluffy abundant plumage of the bulbuls, not the hard, close one of the shrikes. Female much smaller than male as in *Bleda* and *Phyllastrephus*. Chattering voice of bulbuls and brilliant song. Birds of bush and forest; insectivorous.

1. *N. chloris*: Tropical Africa.
2. *N. vireo*: Cameroon to N. Angola and Belgian Congo.

## D. *Criniger* GROUP.

## XI. GENUS *Criniger*.

Temminck, 1920. Type: *Criniger barbatus*.

Bill strong and high, much thicker at the base than near the tip, which is hooked; culmen curved all over; gonys almost straight. Nostrils oval. Rictal bristles well developed. Tarsus short and strong. Wings



and tail rounded. Plumage very long and soft; general color olive yellow or brown, with a conspicuous throat patch of long feathers, white or yellow. Long hair-like feathers on the nape. All species resemble one another closely in color and pattern. Many are fully crested, while others only show indication of a crest, and two none at all. All *Criniger* are forest birds. Their voice is harsh.

1. *C. barbatus*: Upper Guinea.



Text-fig. 10. *Criniger chloronotus chloronotus*.

2. *C. chloronotus*: Lower Guinea and Congo.
3. *C. calurus*: Upper and Lower Guinea to Uganda.
4. *C. olivaceus*: Senegal to Gold Coast.
5. *C. flaveolus*: Himalaya, Assam, Burma, Java, Bali.
6. *C. tephrogenys*: Burma, Siam, Yunnan, Indo-China, Hainan, Malay Peninsula, Sumatra, Borneo, Palawan, Balabac, Camianes.
7. *C. ochraceus*: S. Burma, S. Siam, S. Indo-China, Malay Peninsula, Sumatra, Borneo.
8. *C. finschi*: Malay Peninsula, Sumatra, Borneo.
9. *C. phaeocephalus*: Malay Peninsula, Sumatra and neighboring islands, Borneo.

The grouping of subspecies in the three closely allied and puzzling species, *C. flaveolus*, *C. tephrogenys* and *C. ochraceus*, is difficult and we still have to learn a great deal about them before we can form a final opinion. I adopt here a new grouping proposed by E. Mayr, which I think is the best at the present time; it is following almost exactly one suggested in part by C. B. Ticehurst (*Journ. Bombay N.H. Soc.*, XXXVI, 1933, p. 923-925).

1. *Criniger flaveolus*.  
*flaveolus*: Himalaya, Assam, N. Burma.  
*burmanicus*: C. Burma.  
*xanthizurus*: Java, except East.  
*balicus*: Bali and E. Java.
2. *Criniger tephrogenys*.  
*griseiceps*: C. Burma.  
*henrici*: N. Indo-China, Yunnan.  
*pallidus*: Hainan.

*annamensis*: C. and S. E. Indo-China.  
*robinsoni*: Tenasserim (S. Burma).  
*tephrogenys*: Malay Peninsula, Sumatra (lowlands).  
*gutturialis*: Borneo (lowlands).  
*frater*: Palawan, Balaban, Camianes.

### 3. *Criniger ochraceus*.

*ochraceus*: S. Burma, S. Siam, Cambodia, Cochinchina, N. Malay States.  
*cambodianus*: S. Cambodia (mountains).  
*sacculatus*: Malay Peninsula.  
*sumatranus*: Sumatra (mountains).  
*ruficrissus*: Borneo (mountains).

## XII. GENUS *Setornis*.

Lesson, 1839. Type: *Setornis criniger*.

Bill strong and much hooked, the culmen almost straight and gonys convex. Nostrils and rectal bristles as in *Criniger*. Very long hair-like feathers on nape. General color brown above, yellowish-white below. Rectrices tipped with white on the inner web except central pair. No crest. Legs short, feet small.

In its strongly hooked bill, thick and almost straight, *Setornis* recalls *Nicator*, but it is more depressed and the nostrils, rectal bristles, hair on nape and plumage characteristics are completely different and show its really close relationship to *Criniger*. It is a very peculiar bulbul.



Text-fig. 11. *Setornis criniger*.

1. *S. criniger*: Banka I., Borneo.

## XIII. GENUS *Microscelis*.

Gray, 1840. Type: *Hypsipetes amaurotis*.

Bill slender and long; culmen carinated and slightly depressed at the base, gently curved; nostrils oval; gonys nearly straight; rectal bristles weak or moderate. Nuchal hair short. Legs very short. Wings moderate to long and pointed. Tail long, rounded, square or slightly forked, the rectrices more or less curved outwards in many species. Feathers of the crown erectile, either rounded or pointed and lengthened. Color very variable. Most of these bulbuls live in forest, on high trees in general, some in large flocks; others in scrub and small trees. Their voice is loud and harsh. Frugivorous and insectivorous.



### Subgenus *Tricholestes*.

Salvadori, 1874. Type: *Brachypodius criniger*.

Culmen straight in its basal half, then curved, and hooked, nostrils oval and exposed. Long rectal bristles and very long hairs on the upper back, a unique feature in the family. Wings and tail equal and rounded. General color olive green and brown. Live in brush, bushes and small trees.



Text-fig. 12. *Microscelis criniger criniger*.

1. *M. criniger*: Malay Peninsula, Sumatra, Borneo and neighboring islands.

### Subgenus *Iole*.

Blyth, 1844. Type: *Iole olivacea* = *charlottae*.

Bill strongly carinated, pale brown or gray, like the feet. Feathers on crown normal in shape and only slightly elongated. General color uniform olive green, brown or yellow, paler and brighter below.

2. *M. charlottae*:<sup>5</sup> From Cachar and Sylhet to Burma, Yunnan and Indo-China, Siam, Malay Peninsula, Sumatra, Borneo and neighboring islands, Palawan.  
3. *M. nicobariensis*: Nicobar Islands.  
4. *M. ictericus*: S. W. India and Ceylon.  
5. *M. affinis*: Moluccas, Togian, Sangi, Pel-ling, Banggai, and Sula Islands.

*M. affinis* varies tremendously in size and the smaller forms are strangely similar to *M. ictericus*, while the larger ones, with a particolored tail, dark olive and bright yellow, are not far from *M. everetti*. It is reasonable to assume that they have a Philipinian origin. On account of their distribution, it seems to be difficult to divide these birds into two separate species as one would be tempted to do according to their size and tail pattern.

### Subgenus *Microscelis*.

Gray, 1840. Type: *Hypsipetes amaurotis*.

Bill moderately carinated, of various colors like the feet. Feathers on crown pointed

and more or less elongated. General color very variable, with distinct patterns, never uniform olive green, brown or yellow.

6. *M. everetti*:<sup>6</sup> Philippine Islands (not Luzon).  
7. *M. gularis*:<sup>7</sup> Philippine Islands.  
8. *M. siquijorensis*: Philippine I.: Siquijor, Toblas, Romblon, Cebu.  
9. *M. amaurotis*: Japan and neighboring islands, Korea and E. China (migrant), Formosa, Riu-Kiu and N. Philippine Islands.  
10. *M. virescens*:<sup>8</sup> Himalaya, Burma, S. China, Indo-China, Siam, Malay Peninsula, Sumatra, Borneo, Java.  
11. *M. flavalus*:<sup>8</sup> Himalaya, Burma, Siam, Indo-China, S. China, Hainan, Malay Peninsula, Sumatra, Borneo.



Text-fig. 13. *Microscelis madagascariensis psaroides*.

12. *M. madagascariensis*:<sup>9</sup> Madagascar, Mauritius, Aldabra, Reunion, Seychelles, Comoro Islands, Ceylon, India, Assam, Burma, Siam, Indo-China, C. and S. China, Hainan, Formosa.  
13. *M. thompsoni*:<sup>10</sup> S. Shan States, N. W. Siam, E. C. Burma.

<sup>6</sup> Although both forms are found on Mindanao, I consider provisionally *M. rufigularis* as a subspecies of *everetti* and its lowland and open forest representative. *M. haymaldi*, from Sulu and other southern islands, is exactly intermediate.

<sup>7</sup> *Turdus philippensis* Gmelin is preoccupied by Müller, 1776, and Boddaert, 1783. The next available name is *Phelemon gularis* Pucheran in "Cuvier" Arch. Mus. N. H. (Paris), 1855, 7, 344, pl. 18.

<sup>8</sup> I agree with Deignan that the different forms ascribed by most authors to *malaccensis*, *tickelli*, or *macclandii* are conspecific with *virescens*, and that *castanotus*, *canipennis* and *cinerus* are subspecies of *flavalus*. See Auk, 1942, pp. 313, 314.

<sup>9</sup> I follow Mayr, Deignan, Danis and others in uniting specifically all the closely allied birds formerly referred to *madagascariensis*, *psaroides* and *leucocephalus*.

<sup>10</sup> I do not consider that a bare skin space round the eye and a chestnut patch on the vent are worth a generic separation under the name *Cerasophila*, as *thompsoni* is evidently very close to *M. m. leucocephalus*.

<sup>5</sup> Replaces *Iole olivacea* and *Iole virescens*. See H. G. Deignan, Auk, p. 313. *I. striaticeps* is a synonym of *M. c. palawanensis*. Type, in the Rothschild Collection, examined.

## EXPLANATION OF THE PLATES

## PLATE I.

- Fig. 1. *Spizixos semitorques semitorques*.  
Fig. 2. *Pycnonotus dispar dispar*.  
Fig. 3. *Pycnonotus barbatus xanthopygus*.

## PLATE II.

- Fig. 4. *Pycnonotus sinensis sinensis*.  
Fig. 5. *Microscelis amaurotis amaurotis*.  
Fig. 6. *Microscelis madagascariensis psaroides*.



FIG. 1.



FIG. 2.



FIG. 3.





FIG. 4.



FIG. 5.

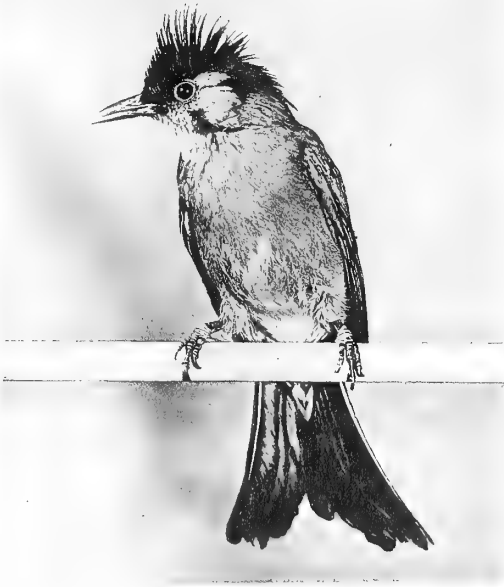
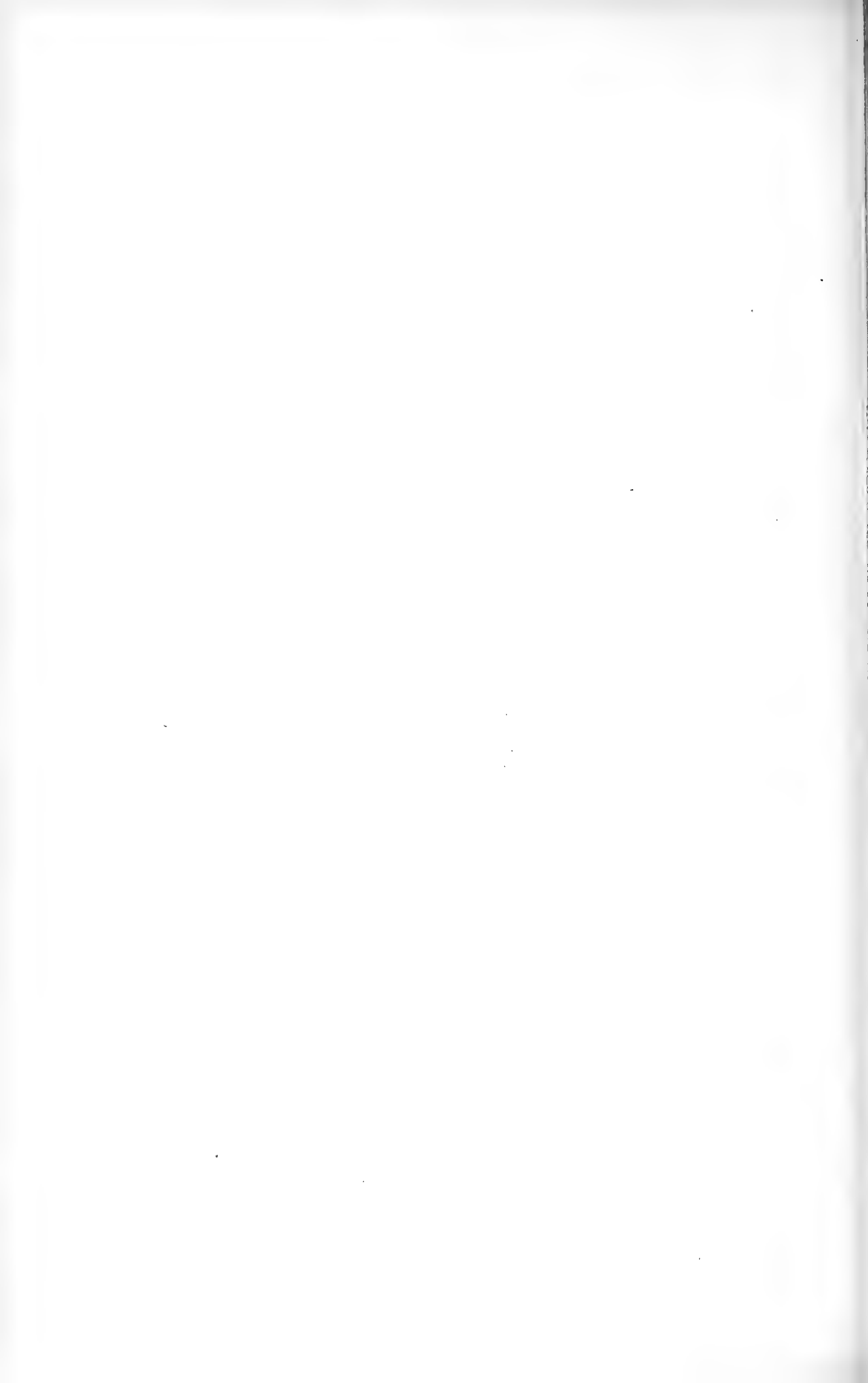


FIG. 6.

A REVISION OF THE GENERA AND SPECIES OF THE  
FAMILY PYCNONOTIDAE (BULBULS).



## 5.

Two New Subspecies of *Pycnonotus cafer*.

JEAN DELACOUR.

(Text-figure 1).

The crested and white-rumped bulbuls, common in cultivated areas and open jungles of India, Burma, Siam, Indo-China and Java, are evidently all conspecific (*Pycnonotus cafer*), but it has long been difficult to trace the transition from the widespread red-vented forms to the yellow-vented races isolated in southern Indo-China and Java: *germaini* and *aurigaster*. An interesting light was thrown on the subject when C. B. Kloss (*Journ. N. H. Sty. of Siam*, 6. No. 3, 1924, p. 291) described a yellow-vented bird from Bangkok as *Molpastes aurigaster thais*. This bird resembles very closely the Javan *aurigaster* in general color, even in the rich golden shade of the under tail-coverts. He, however, was wrong in considering a Chantabun bird as similar, as it is a little browner and less distinctly mottled above and has its under tail-coverts of a decidedly different tone of yellow, approaching the lemon yellow of *germaini*.

Indo-China, N. Siam and S. China, in its smaller size. As one goes south, however, these bulbuls show a tendency to vermilion instead of crimson under tail-coverts. A good series collected by W. P. Lowe (Vernay Expedition) 53 miles east of Um-Phang, in W. C. Siam, shows either crimson, vermilion or orange vents, indicating a mixed intermediate population. At Si-Sawat, some distance to the south, birds have orange vents, while at Ban-Pong, still further south, they have golden-yellow vents, are similar to the Bangkok birds and must be called *thais*. The orange-vented birds have no name, nor have the Chantabun birds with black heads like *thais*, but lemon yellow vents almost like *germaini*. The latter is the dullest race, with a dark brown crown; it is found in all suitable parts of Indo-China, at low and moderate altitudes, south of Tourane in the east, of Napé and Vientiane in the west, and in the neighboring parts of eastern central Siam.

I therefore propose for them the following appellations:

*Pycnonotus cafer schauenseei*.

Intermediate between *P.c. klossi* and *P.c. thais*, in having the under tail-coverts mixed vermilion and yellow, producing an orange color.

Type ♂, No. 1369. Academy of Natural Sciences, Philadelphia. Coll. R. M. de Schauensee, July 6, 1939. Si-Sawat, W. C. Siam.

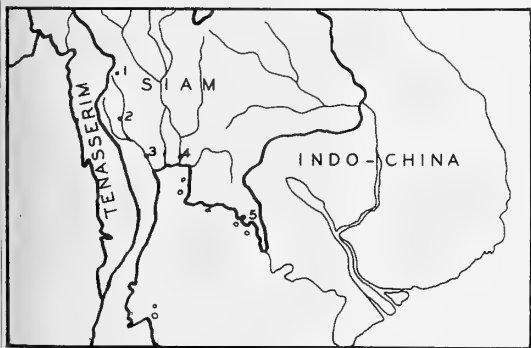
Wing: 88; tail: 79; tarsus: 20; culmen: 18 mm.

Birds from Um-Phang are intermediate and variable, some examples being similar to the Si-Sawat birds. Twelve specimens examined from Si-Sawat and Um-Phang.

Named in honor of Rodolphe Meyer de Schauensee.

*Pycnonotus cafer deignani*.

Intermediate between *P.c. thais* and *P.c. germaini*, in having the black crown and general color of the former, only slightly browner and less distinctly mottled, and



Text-fig. 1. Distribution of races of *Pycnonotus cafer* in southern Siam. 1, Um-Phang (*P.c. klossi* ± *schauenseei*). 2, Si-Sawat (*P.c. schauenseei*). 3, Ban-Pong, 4, Bangkok (*P.c. thais*). 5, Chantabun (*P.c. deignani*).

The nearest relative of these yellow-vented bulbuls certainly is the small, crimson-vented form of central Siam and Tenasserim, *klossi*, differing only very slightly from *chrysorrhoides*, from the Shan States,

lemon-yellow under tail-coverts, only slightly more golden than in *germaini*. Pale tail-tips intermediate in size and color between *thais* and *germaini*.

Type ♂, No. 337.130, U. S. Nat. Museum, Washington. Coll. H. G. Deignan, April 20,

1932. Chantabun, S. E. Siam.

Wing: 90; tail: 80; tarsus: 21; culmen: 18 mm.

Six specimens examined from Chantabun and Chantaburi.

Named in honor of H. G. Deignan.



## 6.

## Eastern Pacific Expeditions of the New York Zoological Society. XXXI.

*Uca schmitti*, a New Species of Brachyuran Crab from the West Coast of Central America.<sup>1</sup>

JOCELYN CRANE

Research Zoologist, Department of Tropical Research,  
New York Zoological Society.

(Plate I; Text-figure 1).

[This is the thirty-first of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of Dr. William Beebe. The present paper is concerned with specimens taken on the Eastern Pacific Zaca Expedition, and, through the kindness of Dr. Waldo L. Schmitt and Dr. Thomas Barbour, with material in the collections of the United States National Museum in Washington and of the Museum of Comparative Zoology at Harvard in Cambridge, Massachusetts.]

Except for nine specimens from the eastern Pacific coast, referred to *Uca mordax* by Dr. Rathbun (1917) and myself (1941), the known range of the species is restricted to the western Atlantic. A reëxamination of each of these nine examples and their comparison with many Atlantic specimens of *mordax* have convinced me that they should be referred to a new, homologous species, described below. With the taxonomic separation of these forms, no species of *Uca* remains which, in the consideration of modern taxonomists, occurs on both the Atlantic and Pacific coasts of the hemisphere.

*Uca schmitti* sp. nov.<sup>2</sup>

Text-fig. 1; Pl. I.

**References:** *Uca mordax* Rathbun, 1917, p. 393 (part.). Crane, 1941, p. 176; text-figs. 2, 3, 4E, 5.

**Description:** This proposed new species, although completely distinct from its Atlantic homologue, *U. mordax*, differs from it noticeably and invariably only in the following characters:

1. The oblique ridge inside the palm is much lower than in *mordax*, and the tuber-

cles with which it is irregularly covered are smaller. Similarly, the tubercles between this ridge and the one at the base of the dactyl are fewer, cover a smaller area and are themselves smaller. These characters alone enable one to separate a mixed group of moderate-sized specimens without the aid of a lens.

2. The palm is relatively deeper than in *mordax*, and the fingers shorter.

3. In contrast to *mordax*, on each of the first three ambulatories there is little pile on the upper sides of the merus and carpus, and none on the lower sides of the manus.

4. Hair on tips of minor chelae usually almost lacking in adults, and always far sparser than in *mordax*.

5. Marginal line of front almost straight, not convex; front appearing slightly broader and shallower than in *mordax*, although this character is variable and cannot be definitely measured.

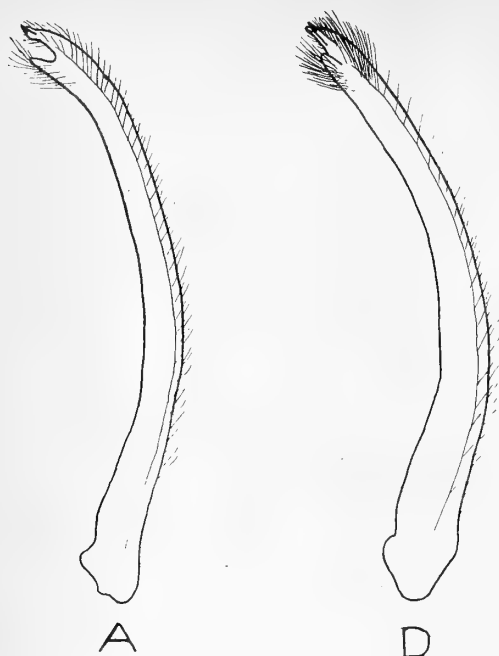
6. Abdominal appendage thicker, with subterminal arm closely applied to tip of appendage, instead of projecting from it, as it does in *mordax*.

7. All four males observed alive were definitely spotted (Crane, 1941, p. 177); none of the many examples of *U. mordax* which I observed in Venezuela ever showed a trace of spots (see paper immediately following, *Zoologica*, Vol. XXVIII, p. 37).

**Measurements:** Male holotype (U.S. National Museum No. 80451), length 13.4 mm., breadth 20 mm.; base of manus to tip of pollex 35 mm. Three male paratypes (U.S. N.M. No. 22306), lengths 13, 14 and 14.5 mm. Four male paratypes (Dept. Tropical Research, N.Y. Zoological Soc. Nos. 381,116, 381,117, 381,118), lengths 9.7, 13, 14 and 14.5 mm. One male (Museum Comparative Zoology No. 5892), length 15.3 mm.

<sup>1</sup> Contribution No. 652, Department of Tropical Research, New York Zoological Society.

<sup>2</sup> Published by permission of the Secretary of the Smithsonian Institution.



*Range:* Acapulco, Mexico, to Golfito, Costa Rica.

*Material:* Holotype: U.S.N.M. No. 80451, San Blas, Tepic Territory, Mex.; 3 paratypes: U.S.N.M. No. 22306, same locality; 4 paratypes: Dept. Tropical Research, N. Y. Zool. Soc.: No. 381,116, San Juan del Sur, Nicaragua; No. 381,117, Negritos Island, Costa Rica; No. 381,118, Golfito, Costa Rica; 1 male: Museum Comparative Zoology, No. 5892, Acapulco, Mexico.

This species is named in honor of Dr. Waldo L. Schmitt, Curator of the Division of Marine Invertebrates at the United States National Museum.

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#### EXPLANATION OF THE PLATE.

##### PLATE I.

Fig. 1. *Uca schmitti*. Male holotype (U.S.N.M. No. 80451), dorsal view. Carapace length 13.4 mm.

Fig. 2. *Uca schmitti*. Major chela of paratype (U.S.N.M. No. 22306), inner view. Carapace length 14 mm.  $\times 2.4$ .

Fig. 3. *Uca mordax*. Major chela of specimen from Caripito, Venezuela (Dept. Trop. Research, N.Y.Z.S. No. 4252a), inner view. Carapace length 14 mm.  $\times 2.4$ .

Fig. 4. *Uca mordax*. Major chela from Caripito, Venezuela (Dept. Trop. Research, N.Y.Z.S. No. 4252b), inner view,  $\times 2.4$ .

Text-fig. 1. Right abdominal appendage of adult male in *Uca mordax* and *U. schmitti*. **A**, *mordax*, outer lateral view; **B**, same, tip, outer lateral view; **C**, same, tip, anterior view; **D**, *schmitti*, outer lateral view; **E**, same, tip, outer lateral view; **F**, same, tip, anterior view. **p**:

genital opening; **a**: subterminal arm. (Exact numbers of hairs not shown in full-length views, although apparent proportions and exact locations are indicated; hairs omitted from drawings of tips).



FIG. 1.



FIG. 2.

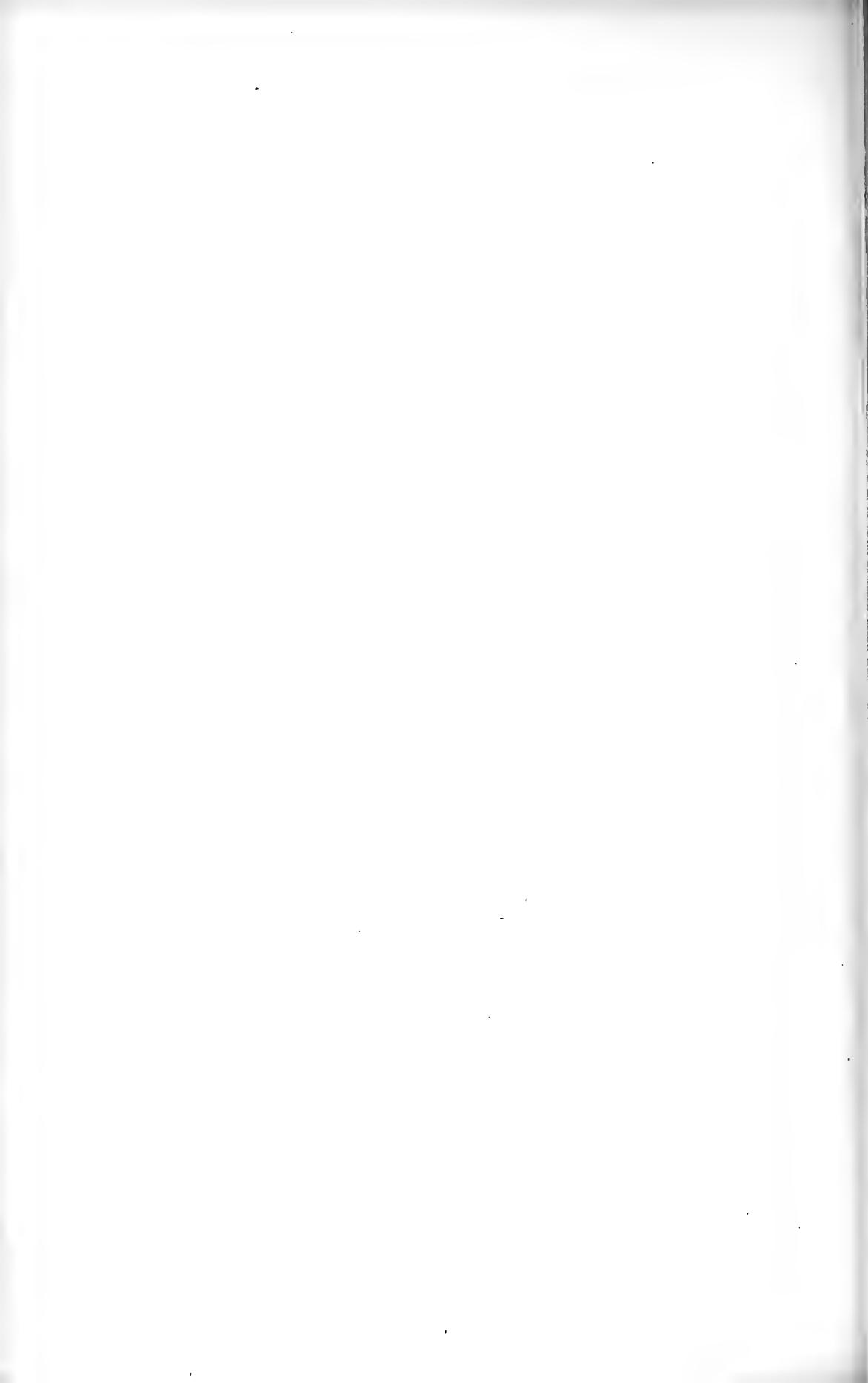


FIG. 3.



FIG. 4.

UCA SCHMITTI, A NEW SPECIES OF BRACHYURAN CRAB  
FROM THE WEST COAST OF CENTRAL AMERICA.



## 7.

Crabs of the Genus *Uca* from Venezuela.<sup>1</sup>

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(Plate I; Text-figure 1).

[This is a contribution from the Forty-third or Venezuelan Expedition of the Department of Tropical Research of the New York Zoological Society made under the direction of Dr. William Beebe. The expedition was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

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## I. INTRODUCTION.

The present study is based on 1,049 specimens of *Uca* collected on the Venezuelan Expedition of the Department of Tropical Research of the New York Zoological Society, under the direction of Dr. William Beebe. The expedition extended from February to September, 1942, with headquarters at Caripito, in northeastern Venezuela.

The specimens are distributed among five species, of which two are apparently new to science, and were taken in four general localities: the Caripito region of the San

Juan River; the swamp near the mouth of the San Juan; the Pedernales region at the mouth of the Caño Manamo at the southern end of the Gulf of Paria; and the Maracaibo region, in western Venezuela. For the excellent and extensive collection made at Maracaibo, I wish to express my thanks to Mr. Henry Fleming, the expedition's entomologist, who collected the material for me during a week's stopover in that locality. During the course of collecting the remainder of the crabs, I was able to make a number of ecological observations, which are incorporated in the present report, including the displays of four of the five species taken.

For general working methods, and for definitions of measurements and special terms, refer to Crane, 1941, p. 148. The making of a series of 16 mm. color motion pictures of displaying fiddlers at Pedernales was the only new addition to the working procedure. Detailed drawings of abdominal appendages are presented, since the genital organs are proving, in this as in other groups of animals, to be of definite aid in taxonomy; more work needs to be done, however, before basic structural plans and their evolutionary significance can be adequately described and evaluated.

Miss Rathbun's synonymy (1917) has been accepted throughout, except in regard to *U. mordax* (see p. 38).

## II. ECOLOGY.

*Habitat:* All of the crabs were taken from slightly brackish river banks and delta shores. Although each locality was under tidal influence, the salinity in all cases was very low. The majority were collected during the rainy season in the summer months, so that the salinity was at its minimum. Adequate series of salinometer readings were not made, but Table I will give a general idea of conditions.

<sup>1</sup> Contribution No. 653, Department of Tropical Research, New York Zoological Society.

TABLE I.

Place	Date	Season	Tide	Salinity (cf. with normal sea water)
Caripito	Apr. 10	Dry	2 hrs. after high	0.6%
Near mouth San Juan R., 8 miles above bar	Apr. 10	Dry	High	1.2%
Pedernales	Aug. 25	Rainy	High	.23%
Pedernales	Aug. 26	Rainy	1 hr. after low	1.2% <sup>2</sup>
Maracaibo, Yacht Club	Sept. 7	Rainy	High	2.0%

In spite of these relatively small differences, the five species taken group themselves definitely into a series, the proportions shifting from river to near river mouth to Maracaibo mud flats in a way that cannot be wholly accounted for by changes in vegetation, soil or amount of light, since in these respects certain stations in each of various localities were very similar. The occurrences of the crabs may be tabulated as in Table II.

The second habitat (near the river mouth) was collected only during a two-hour period on a single day at one spot, in deep shade,

(both in the semi-shade of mangroves and on the open flats) around Maracaibo, *mordax* was completely absent while *pugnax rapax* was far and away the dominant form. Of 526 specimens of *Uca* collected by Mr. Fleming at Maracaibo from five different stations, giving as varied habitats as possible, all except 15 were *pugnax rapax*, the remainder being *murifecenta*, the proposed new species taken also near the mouth of the San Juan and at Pedernales.

At Pedernales, the only locality where all five species were taken, the preferences for

TABLE II.

	<i>mordax</i>	<i>pugnax rapax</i>	<i>murifecenta</i>	<i>cumulanta</i>	<i>maracoani</i>
River: Minimum salinity; mangroves rare: Caripito, Guanoco.	Dominant	—	—	—	—
Near river mouth: mangroves dominant: San Juan R., 8 miles above bar.	yg. only (April)	Rare	Dominant	—	—
Lower delta swamp: mangroves and marsh grass only: Pedernales, at mouth of Caño Manamo.	Abundant	Common	Rare	Abundant	Common
Tidal flats: mangroves adjacent or distant; marsh grass sometimes present: Maracaibo.	—	Dominant	Rare	—	—

back from the banks, among the highest mangroves; hence the results obtained there would doubtless be considerably modified by more extended collecting in the vicinity.

The other regions, however, were extensively collected, and although additional species would almost certainly be added by exhaustive collecting over a protracted period, the relative abundance indicated by the table would doubtless in general hold true. The major fact appearing is that up rivers, toward the limit of the *Uca* range, only *U. mordax* occurs, but that it is here extremely successful; all along the banks of the upper San Juan and its tributaries, and many yards back in the adjacent swampy land, *mordax* was exceedingly abundant, the colonies often lining the banks in practically unbroken series. At the opposite end of the brackish water habitat, on the tidal flats

particular habitats could be best compared. Here the differences noted in Table III were obvious, and these observations tallied with preferred habitats in the other localities.

*Size:* No statistical work has been done as yet, but it is interesting to note that adult *pugnax rapax* taken at Maracaibo from the No. 2 type of habitat—i.e., from close to or among mangroves—were on the average definitely larger than those from the barren mud and sandy-mud flats in the same neighborhood.

*Breeding:* Apparently in Venezuela the main breeding season is in the spring. *U. mordax* at Caripito was displaying vigorously from February throughout April, and ovigerous females were seen at this time. Between May and September there was progressively less waving seen, and by late summer it appeared to have practically died out, although during the third week in August, at Pedernales, it was continuing in desultory fashion. The season of *pugnax*

<sup>2</sup> The apparently contradictory results obtained at Pedernales, where the salinity near low tide was almost six times more than at a high tide near full moon, is doubtless due to the erratic currents in the neighborhood.

TABLE III.

Key					
	<i>mordax</i>	<i>pugnax rapax</i>	<i>murifecenta</i>	<i>cumulanta</i>	<i>maracoani</i>
X, Preferred					
X, Present					
—, Absent					
1. Deep shade, among mangroves	X	—	X	—	—
2. Open sunny, or semi-sunny, mud patches among mangroves and/or grass tufts	X	X	X	X	—
3. Open mud flats	X	X	—	X	X
4. Open mud flats with surface layer of sand, or sand and pebbles	X	X	—	X	X

*rapax* apparently corresponds exactly to that of *mordax*. The full breeding season of *murifecenta*, judging by the proportion of ovigerous females, occurred in April; no ovigerous examples were taken at the other localities where it occurred, in August and September. No ovigerous females of either *maracoani* or *cumulanta*, collected only at Pedernales in late August, were found, although the males were displaying vigorously compared to those of other species, and the females showed response, especially in *cumulanta*; in *maracoani* the final stages of courtship and response were not observed.

### III. PHYLOGENETIC NOTES.

It is not possible at this time to analyze the relationships of western Atlantic *Ucas* as was done in the case of the eastern Pacific forms (Crane, 1941), and consolidate the two studies, but the present collection does shed further light on this general problem.

In the first place, the conclusions reached in that paper, in regard both to the divisions of the fiddler crabs into phylogenetic groups (*loc. cit.*, p. 165) and to the relationships of these species traceable through courtship displays as well as physical characteristics, are corroborated and extended. The coloration and display of *maracoani* fitted in with those previously observed on the Pacific coast among others in Group 1, while the rapping phase of display in *cumulanta*, the proposed new species referable to Group 4, had as obvious affinities in display to members of that group in the Pacific as it did in its physical attributes; in addition, *cumulanta* built shelters similar to those made by *beebei*, *latimanus* and *terpsichores* in Group 5.

The remaining three species of the Venezuelan collection, *mordax*, *pugnax rapax* and *murifecenta*, all belong to Group 2, and were of special interest since I had not previously had an opportunity of observing the display of members of this group. The new species, *murifecenta*, was not seen waving,

but in both of the other species the main display characteristics consisted of a series of three to five jerks with the major cheliped, accompanied or followed by kicking out and vibration of two or more ambulatories. Also, both displays were exceptionally slow and deliberate, and no brilliant or even striking colors were assumed, general lightening of the carapace, and the assumption of dull ochres or oranges on the major cheliped being the maximum change. Both the slowness and the dullness are in contrast to the display characteristics of the more highly developed species of the other groups, and lends additional evidence to the theory already proposed (*loc. cit.*, p. 166) that members of Group 2 are relatively primitive. Another interesting point is that they fail to clean more than their eyes, frontal region and chelae of mud before displaying, in great contrast especially to the end members of other groups. A final observation in regard to this group is that its members appear much more subject to individual variation than do those of the others.

Some adult females of both *mordax* and *murifecenta* were observed to have walls about their holes similar to those occasionally made by the females of *stenodactyla* (*loc. cit.*, p. 196), but the males built no shelters of the type made by *minax* in the north (which are quite different from the hood-like forms built by *cumulanta* and members of Group 5). The entire question of shelter-building still remains one of the most puzzling problems to be solved in connection with these crabs.

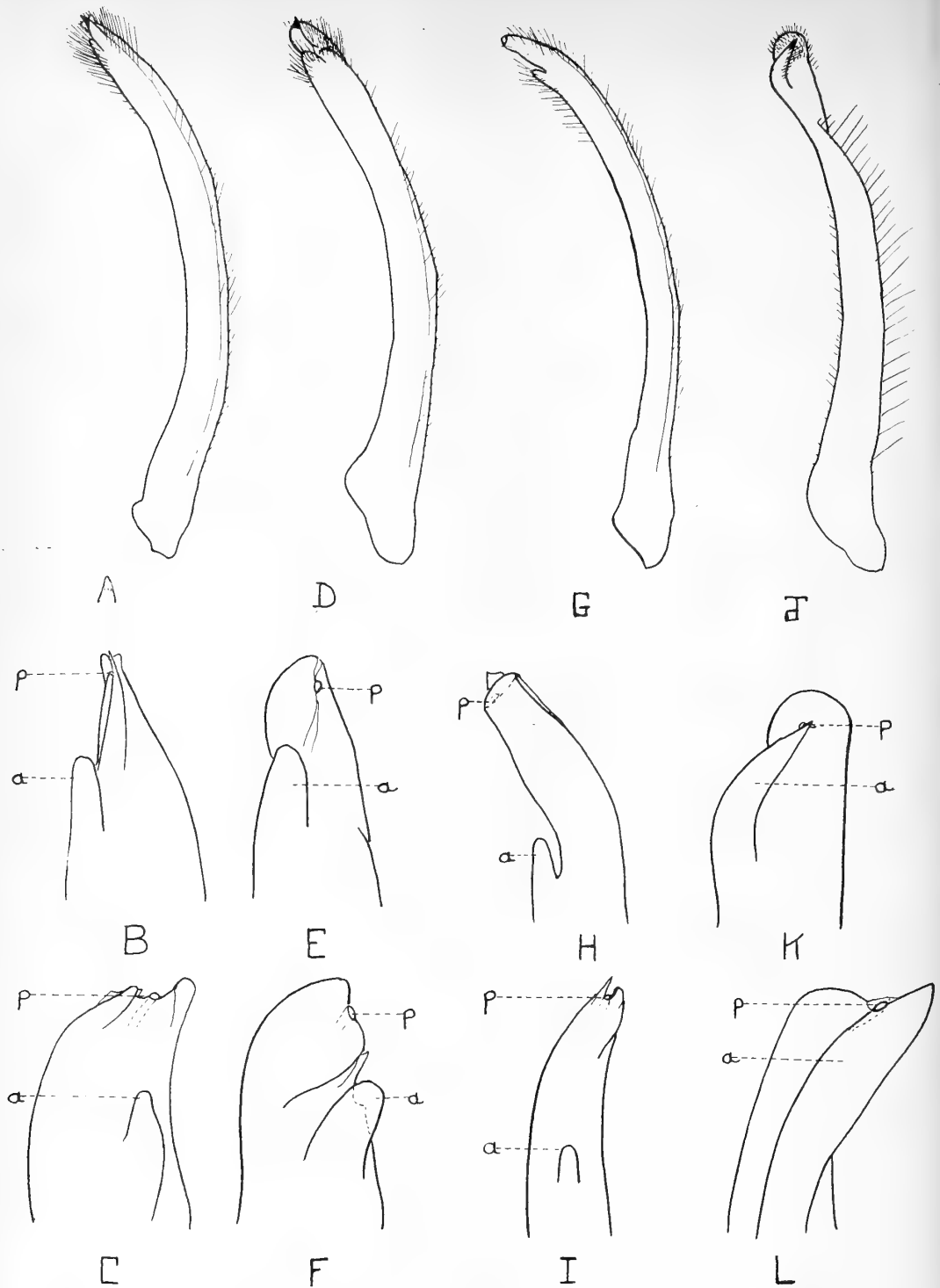
### IV. SPECIES OF *Uca* TAKEN BY THE VENEZUELAN EXPEDITION OF THE NEW YORK ZOOLOGICAL SOCIETY.

*Uca maracoani* (Latreille, 1802-1803).

Text-fig. 1J,K,L,

References: *Ocypode maracoani* Latreille, 1802-1803, p. 46.

*Uca maracoani*, Rathbun, 1917, p. 378; pl. 130, figs. 2, 3; pl. 131, fig. 3.



Text-fig. 1. Right abdominal appendages of adult males in *Uca*. **A**, *pugnax rapax*, outer lateral view; **B**, same, tip, outer lateral view; **C**, same, tip, anterior view; **D**, *murifecenta*, outer lateral view; **E**, same, tip, outer lateral view; **F**, same, tip, anterior view; **G**, *cumulanta*, outer lateral view; **H**, same, tip, outer lateral view; **I**, same, tip, anterior view; **J**, *maracoani*, outer lateral view; **K**, same tip, outer lateral view; **L**, same, tip, anterior view. **p**: genital opening; **a**: arm. (Exact numbers of hairs not shown in full-length views, although apparent proportions and exact locations are indicated; hairs omitted from drawings of tips).



*Range:* Previously known between Cayenne, French Guiana, and Rio de Janeiro, and, by Sloane's record, from Jamaica. The present record extends the range to eastern Venezuela.

*Local Distribution:* Found on open tidal sandy mud shores in river deltas; water slightly brackish.

*Supplementary Specific Characters:* Abdominal appendage of male slender and tapering, save for a slight subterminal constriction at the beginning of the strongly curved distal portion. Subterminal arm strongly chitinated, spinous, crossing in front of densely haired tip. Female with moderate-sized tubercle on external side of genital opening. Spooned hairs on merus of external maxillipeds with the strong basal spine typical of species in Group 1, but with pectinations better developed than usual in this group.

*Measurements:* The 18 specimens taken include the following extremes of length: largest male, 18 mm.; largest female (immature) 13 mm.; smallest male, 9 mm.; smallest female, 6.3 mm.

*Color:* Displaying males observed through binoculars: Carapace dull grayish-purple, never free from mud, except on frontal region and behind eyes. Anterior margins of eyebrows scarlet orange. Major cheliped: merus, carpus and base of manus grayish-brown, shading distally into dull orange; pollex scarlet orange; dactyl, outer side, purplish-orange to scarlet orange; dactyl, inner side, usually iridescent purple with orange reflections. Minor manus and chelae scarlet orange. Mani or all ambulatories dull scarlet orange. Subocular and pterygostomian regions bright purple. Immature males with major pollex and dactyl orange without scarlet tinge. Females plain brown.

*Display:* At beginning of display all ambulatories are stretched upward, elevating body. Major and minor chelipeds start from position folded in front of mouth, at mouth level. The manus and chelae of both chelipeds are then extended upward and outward, with fingers kept extended throughout, and brought down into position. With each gesture the second ambulatory, the second and third, or the third only on the minor side, and, usually the first and second on the major side are lifted from the ground and spread sideways. During display a few steps are usually taken, either side-wise or in a circle, the crab facing outward. Each display lasts about three-quarters of a second, and the next in the series follows almost at once. One day, shortly before high tide, I noticed a great deal of apparently aimless racing about on the part of these crabs; no females were visible as special stimulus, as in the case of *U. stenodactyla* (Crane, 1941, p. 196).

Males were displaying fairly continuously between August 23 and 27, the only period of observation, and showed interest in females; final stages of courtship were not seen, however, nor were ovigerous females taken.

*Material:* A total of 18 specimens was taken at Pedernales, Venezuela (Cat. No. 42414).

### *Uca mordax* (Smith, 1870).

*References:* *Gelasimus mordax* Smith, 1870, p. 135, pl. 2, fig. 3; pl. 4, figs. 4 and 4a.

*Uca mordax*, Rathbun, 1917, p. 391, text-fig. 166, pl. 134, figs. 3 and 4. (*Partim*: not Pacific specimens).

Not *Uca mordax*, Crane, 1941, p. 176, text-figs. 2, 3, 4e.

*Range:* From the Bahamas and Gulf of Mexico to Rio de Janeiro.

*Local Distribution:* Found among mangrove roots and mucka mucka, preferably not in deep shade, and on the open muddy banks of slightly brackish streams. Sometimes they live in moist, muddy ground many yards back from the river edge, in areas inundated only at spring tides. This is the typical, abundant fiddler of the banks of rivers well above their mouths and of the upper delta areas.

*Supplementary Specific Characters:* Spoon-tipped hairs on merus of second maxilliped almost or completely lacking; woolly hairs moderate in number. Ischium of third maxilliped with central groove very broad, shallow, parallel to inner groove, with which it tends to merge basally, although it is scarcely traceable so far.

Minor chelae about as long as palm with fairly strong serrations in middle third; distal third horny, dilated, the tips articulating perfectly; gape slight, extending to articulation. Hairs moderately well developed, even in large specimens, both distally and in the usual inner oblique rows; there are in addition a few forming an external row.

Suborbital region hairy.

Abdominal appendage of male slender, with a short arm projecting from it at an acute angle (Crane, 1943, p. 32, text-fig. 1A, B, C.). Gonopore of female without tubercle, or with at most a rudimentary marginal swelling.

*Measurements:* The 246 specimens taken include the following extremes of length: largest male, 15.5 mm.; largest female 14.5 mm.; ovigerous females, 8.4 to 12.5 mm.; smallest male, 2.5 mm.; smallest female, 2 mm.

*Color:* Displaying males: Carapace varying from slaty through yellowish-gray to whitish. Manus of major cheliped usually faintly yellowish; fingers of both major and minor chelipeds creamy white. Front of all

ambulatories pale bluish in some of the specimens taken around Caripito; legs otherwise brownish. Since these crabs appear never to clean more than their eyes and the fingers of both chelipeds, the colors are much dimmer than would otherwise be the case. Females and young brownish. There is never the least trace of the spots, in either living or dead specimens, which are so characteristic of *U. schmitti*, the homologous Pacific form.

**Display:** The carapace is elevated on legs stretched up to tiptoe, chelae held high, crooked in front of mouth. Major cheliped is raised upward in three or four jerks, which are immediately followed by three or four jerks down, without pause at the peak, and with scarcely any pause afterward, between displays in a single series. One or two ambulatories of either or both sides are raised and kicked outward at peak of display. Both major and minor chelae are kept ajar during the entire period, and during each display the minor cheliped makes a circular gesture corresponding to that of the major. When possible, some small eminence is chosen for display, the crab sometimes moving a few steps in either direction during display, but apparently never revolving. About five seconds is the average time required for a single display, although when the crab is much excited by a female, it may be much faster, even as much as two to the second. In the latter case, there may be long waits between displays, in which the crab poses motionless with the major cheliped held overhead. The height of the courtship excitement seems to be indicated by the completion of the display with rapid vibrations of the third, or second and third, ambulatories on each side, after their kicking routine.

One male, with the major cheliped abnormally regenerated, with exceedingly small, crooked chelae, displayed vigorously, but the waving consisted of repeated circular motions with the cheliped held aloft, and with the characteristic jerking absent. This crab was not observed to arouse any interest among nearby females.

**Breeding:** The faster, more complex displays described in the paragraph before the last were seen only at Caripito, between February and April, and not at Pedernales in August, when the breeding season was definitely waning and only a few males displaying. During several days' concentrated collecting in this locality, only four ovigerous females of this species were taken; at Caripito in the spring they were relatively much more numerous. One of these Pedernales ovigerous females had her hole surrounded by a three-inch wall of pellets. The eggs, which measure .51 mm. in diameter after having been preserved in alcohol, number

between about 3,000 and 10,000, depending on the size of the crab. Near the mouth of the San Juan river in April only young, none more than 10.5 mm. long and the majority much smaller, were taken. It may be that they are not established here, for undetermined reasons, but that young get washed down from the great colonies further up-river.

**Discussion:** The Pacific crabs referred by me to this species in 1941 (p. 176), as well as those in the Museum of Comparative Zoology and at the U. S. National Museum (No. 22,306) referred to it by Rathbun (1917, p. 393), form the basis of a new, homologous species. Its description, along with the differences separating it from *U. mordax*, have been published in the paper immediately preceding this one (Crane, 1943, p. 31).

The present Venezeulan collection of *mordax* is typical of the species. There is some variation in the ornamentation of the palm, but most of this is due to age; in the young the tubercles in many specimens are relatively smaller, while in the very old they are sometimes almost lacking on the oblique ridge. There are also small variations in the width and shape of the front of the carapace. None of these variations, however, can be shown to depend on geographical location, or on local habitat.

The females of *mordax* are easily distinguished from those of *pugnax rapax*, which sometimes approach each other in width of front in this sex, by the total absence or extremely rudimentary condition of the tubercle at the genital opening. An examination of the Liberian female (U.S.N.M. No. 21847), referred questionably to this species by Miss Rathbun (1917, p. 393), has convinced me that it cannot be *U. mordax*: although it is small (7.9 mm. in length), it appears adult and has a well developed genital tubercle. In addition, the orbits are less slanting than in female *mordax* of similar size, and there is less pile on the ambulatories.

**Material:** A total of 246 specimens was taken in the San Juan River (at Caripito, Cat. no. 4252; Guanoco, Cat. no. 4254; and near its mouth, 8 miles above the bar, Cat. no. 42166); and at the mouth of the Caño Manamo (at Pedernales, Cotorra Island and Tapure), Cat. no. 42415.

#### *Uca murifecenta* sp. nov.

Pl. I, Figs. 1-3; Text-figs. 1D,E,F.

**Diagnosis:** Carapace moderately convex with conspicuous patches and reticulations of pile; front behind eyes broad and shallow, but considerably less than one-third width of carapace; orbits little oblique; antero-lateral margins convex, curving gradually backward; minor chelae about as long as palm,

with fairly strong serrations in middle third, gape moderate, decreasing distally to perfectly articulating tips. Major palm with oblique ridge poorly developed, covered with band of low, small tubercles, only reaching carpal cavity; rows of tubercles at base of dactyl diverging and inner surface of palm granulate, as in *mordax*. Merus of ambulatories slightly enlarged in male, more so in female. Spoon-tipped hairs absent on merus of second maxillipeds. Suborbital region partly naked.

*Description:* A moderately small species. H-form depression shallow, but marked with pile; additional patches and reticulations of pile on hepatic and branchial regions, and sometimes on protogastric and mesogastric as well; surface of carapace otherwise smooth. Pile also present on upper surface of all segments of ambulatories; rare on under surface of manii as well in male, but rudimentary in female. In addition, the ambulatorial manii and carpi in the male have a number of conspicuous long, soft hairs.

Carapace moderately convex, widest behind antero-lateral angles. Upper margin of orbit scarcely oblique. Anterior part of lateral margins convex and curving gradually backward; the margin thereafter curving sinuously inward, ending at a point opposite middle of cardiac region. Front between posterior margins of eyestalks about midway between one-fourth and one-third maximum width of carapace, very shallow, almost truncate. Lower margins of both front and orbit visible in dorsal view. Eyebrow moderately narrow, steeply inclined. Lower margin of orbit with crenulations poorly developed, concealed by hair and pile. Suborbital region with general, thin, delicate covering of pile, easily dislodged, and an anterior marginal band of hairs. Segments of male abdomen distinct.

Spoon-tipped hairs on merus of second maxilliped absent. Woolly hairs plentiful. Ischium of third maxilliped with shallow central groove well developed except in a few large specimens, almost confluent with inner groove basally.

Minor chelae with moderately strong serrations in middle third; distal third corneous, dilated, the tips articulating perfectly; gape slight to moderate, decreasing steadily to the articulation.

Hairs in an irregular oblique row across inner and outer surfaces of each finger, scanty except for an internal and external tuft distally.

Large cheliped of male with arm rugose, with pile between rugosities. Wrist weakly tuberculate, with a row of about four low teeth on upper margin; a patch of pile on upper outer surface, covered by manus in flexion of cheliped. Hand less than one and a half times longer than wide with rows of

low tubercles—double or triple above, single below—forming low carinas on upper and lower margins. Close-set, low, moderate-sized tubercles covering outer upper surface; but so low and small on lower half that surface appears smooth. Inner face with oblique ridge low and weak, covered with a band of tubercles, not set in definite rows and stopping at carpal cavity in a cluster of several large tubercles. Upper margins of carpal cavity marked by a ridge of coalesced granules. A row of well developed tubercles extends from proximal part of upper margin of pollex obliquely up and back across distal part of palm, dying out well below dorsal margin. Space between this ridge and carpal cavity filled with strong, low tubercles, leaving smooth only the concave area just below dorsal margin and the similar concave space at base of pollex. A short row of several small tubercles parallels base of dactyl. Dactyl almost one-third longer than palm, tuberculated dorsally in proximal region, curving strongly downward beyond tip of pollex. Latter more slender than dactyl, tapering. Gape moderate. Many low, blunt teeth on each finger; about four enlarged ones scattered at intervals on dactyl, the largest being less than one-third the distance to top; pollex with one enlarged tooth about midway to its tip, and one at extreme tip; in addition a pair, beyond this, are directed distally, at right angles to the normal teeth.

Merus of ambulatory slightly enlarged in males, considerably in females; that of third leg extends about a fifth of its length beyond antero-lateral angle when laid forward.

Abdominal appendage of male thick, scarcely tapering, with a thick, subterminal arm paralleling it, not protruding laterally. Genital opening of female marked by a large tubercle.

*Measurements:* Male holotype, length 14.5 mm., breadth 20.5 mm., base of manus to tip of pollex 32 mm.; 5 male paratypes, lengths 11 to 12.5 mm.; 5 ovigerous female paratypes, lengths 8.2 to 13.5 mm.; 1 non-ovigerous female paratype, length 13.5 mm.; largest male, length 15.6 mm.; smallest male, length 6.9 mm.; smallest female, length 6.9 mm. In addition to the above, 41 males, 3 ovigerous females and 17 non-ovigerous females of intermediate lengths were taken.

*Color:* Brightest males, free, but not displaying: Dull rusty orange above, with major manus and chelae moderately bright lemon yellow. Brightest females dull rusty orange above, rest of body and legs brownish. Most crabs of both sexes, however, were dull brownish. The majority of those captured turned from brown to faintly rusty in the refrigerator over night. Eggs magenta.

*Walled Holes:* Large crabs, including the brightest specimens of both sexes, were seen resting on top of, or partially leaning on,

the broad flanged wall surrounding the mouth of some of the holes. The majority of these walled holes seemed to belong to large females, often ovigerous. The largest structures were  $2\frac{1}{2}$  inches high by 2 inches across the widest part, those of smaller crabs being in proportion. A number of pairs of contiguous turrets were seen, a large male and female in each pair. Turrets were built of pellets large in proportion to the crab, up to 5 mm. across. Compared to the numbers of this species, which was dominant near the mouth of the San Juan, turrets were few in number.

**Breeding:** Ovigerous females were common near the mouth of the San Juan River on April 10. The males were not seen displaying, although this may have been solely due to the fact that there was no opportunity for quiet, undisturbed observation. No very young crabs were taken here, and no ovigerous specimens were taken at Pedernales and Maracaibo, in August and September, the other localities where the species was collected. The eggs of San Juan specimens, which measure .51 mm. in diameter after having been preserved in alcohol, number between about 3,200 and 7,000.

**Affinities:** *U. murifecenta* belongs in the broad-fronted group of crabs having the antero-lateral margins curving gradually backward, and few or no spoon-tipped hairs on the merus of the second maxilliped, and described under the general designation of Group 2 in a previous paper (Crane, 1941, p. 166); it includes *pugnax*, *mordax*, *brevifrons*, etc. The present proposed species is probably most closely related to *mordax*, resembling it closely in the general shape of body and cheliped, and in the ornamentation of the major manus. It differs, however, in the presence of pile on the carapace, in the much weaker, sometimes obsolescent, oblique ridge inside the manus, with the tubercles considerably finer; in the more truncate, narrower front, in the shape of the abdominal appendage of the male, and in the presence of a large tubercle beside the genital opening in the female. The ornamentation inside the manus, with the reduced ridge covered by granules or tubercles which tend often to run into those between the carpal cavity and the diverging ridges at base of pollex and dactyl, resembles also that of *pugnax*. As a field character, the presence of pile is excellent, since it is present in none of the other related species hitherto described. Although pile is much less abundant on the females than on the males, and in general somewhat less plentiful on the Maracaibo specimens than on those from eastern Venezuela, still, when looked for, it is unmistakably distinct.

**Local Distribution:** Near the mouth of the San Juan River, the only locality where this

species was abundant (here it was dominant), it lived in the shade of tall (75-foot) mangroves and six-foot ferns, from fifteen feet to many yards back from the river bank. This locality was not visited at extreme high tide, but it seems certain that it is inundated only at spring tides; an hour before an ordinary high tide, however, the water came to within one foot of the surface one hundred and fifty feet from shore; hence the surface, always in deep shade, never really dries out even in April, the end of the dry season. At Pedernales the species was taken in similiar shady, muddy regions among mangroves. In Maracaibo a few were taken on flats shaded only by tussocks of marsh grass. The salinity in each of these localities is low, but the absence of the species from the San Juan up at Caripito indicates that it cannot stand water as fresh as does *mordax*.

**Material:** A total of 76 specimens, including the male holotype five male paratypes and six female paratypes was taken in Venezuela near the mouth of the San Juan River, 8 miles above the bar (57 specimens, including the type series); from Pedernales (3 specimens); and from Maracaibo (16 specimens). Cat. nos. 42167 (holotype), 42417 (paratypes), 42418 (remaining specimens from San Juan), 42416 (Pedernales) and 42419 (Maracaibo).

The name *murifecenta* is given to this species in reference to its habit of making walls.

### *Uca pugnax rapax* (Smith, 1870).

Text-figs. 1A,B,C.

**References:** *Gelasimus rapax* Smith, 1870, p. 134, pl. 2, fig. 2; pl. 4, fig. 3.

*Uca pugnax rapax*, Rathbun, 1902, p. 7; 1917, p. 397, pl. 140.

**Range:** From Miami, Florida and the Gulf of Mexico to Rio de Janeiro.

**Local Distribution:** Tidal salt marshes, often with sandy or pebbly upper layer over the usual muddy substratum, either bare and open, or among tussocks of marsh grass; sandy mud shores of bays and river mouths; sometimes in shade among mangroves with *mordax*, but in general requires saltier water than the latter, although their ranges overlap. See Oliveira, 1939, for a detailed analysis of a typical habitat in Brazil.

**Supplementary Specific Characters:** Spoon-tipped hairs on merus of second maxilliped moderate in number, strongly developed, but variable, usually between about 70 and 120; two groups of specimens, otherwise indistinguishable from the rest, from near the mouth of the San Juan among mangroves and from a single muddy shore with grass tussocks in the Pedernales region, had the spoon-tipped hairs fewer in number than others of similar size—as few

as 25—and the spoon tips themselves more elongate and delicate; these groups were taken in the two most shady locations where the species occurred. Woolly hairs moderate in number. Ischium of third maxilliped with central groove very broad, shallow, parallel to inner groove with which it tends to merge basally, although it is scarcely traceable so far.

Minor chelae as in *mordax*. Suborbital region mostly naked except for an anterior border of hair and pile.

Abdominal appendage of male thick, scarcely tapering, with a thick, short, distal arm paralleling it, not protruding laterally. Genital opening of female marked by a moderate-sized tubercle, sometimes reduced in ovigerous specimens.

Front of male appears slightly deeper and more tapering, therefore narrower, than that of female. In details of shape of carapace and ornamentation of cheliped, this species is variable, as usual in Group 2 species (see page 00).

*Measurements:* The 645 specimens taken include the following extremes of length: largest male, 18 mm.; largest female, 15 mm.; ovigerous females, 8.06 to 14.5 mm.; smallest male, 3.55 mm.; smallest female, 4.9 mm.

*Color:* Displaying males (observed at Pedernales only): Carapace grayish-white to buffy yellow, brightest on front; no part of it except front ever really free from mud. Underparts duller. Major cheliped—merus, carpus and basal half of manus—brownish, changing on distal half of manus to moderately bright apricot buff. Distal to this both fingers are light apricot orange fading distally to creamy white. Manus and fingers of minor cheliped creamy white, rest of it and all ambulatories brownish, never cleaned of mud in displaying. One male had patches of bright green algae on upper outer side of major merus and upper outer sides of manus of all ambulatories. Females and non-displaying males, observed at Pedernales and near mouth of San Juan River, dull brownish, faintly spotted.

*Display:* In full display this crab, although the movements are relatively slow compared with more marine forms, is exceptionally dramatic: The display starts with body elevated on extreme tiptoe, chelae held flexed in front of mouth, well above ground. Major cheliped is raised upward in three jerks, held at topmost stretch so that accent of display is here, held for a dramatic instant, and then swung smoothly and swiftly obliquely down to the flexed starting point. When the crab is not displaying strongly, however, or when apparently tired toward the end of a long series, there are sometimes one or two small jerks on the end of the downward stroke. In any case, the

display is at once repeated, without pause. Fingers of major cheliped are opened in each display; those of minor stay open throughout. During display any one or two ambulatories on both sides (including rarely the fourth, at least on major side) may be lifted and kicked outward at peak of display. The crab may move a few steps, usually toward major side, or hold still, but does not revolve. There are up to at least 20 displays in each series. Only the eyes, front, chelae and part of the major manus are kept clean, but these are always immaculate before display begins. About six seconds are required for each display: three to five in the elevation of the cheliped, one in the pause at the apex, and one-half a second on the way down.

*Breeding:* Three of the four ovigerous females were taken in April near the mouth of the San Juan River, and measure between 8.06 and 10.5 mm. Only four other females were taken in this station. The fourth ovigerous specimen, 14.5 mm. long, was taken at Pedernales the third week in August, the only ovigerous female among a total of 36 females collected from this locality. The first week in September not one of 70 females collected at Maracaibo carried eggs. Hence a spring breeding season is indicated in Venezuela. There was opportunity for observing display only at Pedernales in August; here it was desultory or completely lacking in most adults, strong in very few. The eggs, preserved in alcohol, measure .51 mm. in diameter, and number between about 1,800 and 19,000.

*Discussion:* In shape of front and antero-lateral margins as well as in details of ornamentation of the inside of the manus, and development of teeth on fingers, this form is somewhat variable, as Rathbun has already noted, and as is true also of other species in this group (*U. mordax*, etc.). I can detect no geographical distinctions, however, which would justify making further specific or subspecific distinctions. The most interesting result of this large collection is the observation that in general the specimens taken on sandy-mud superstratum over mud, in the open sunlight but with vegetation nearby, grow to larger size than those either in adjacent deeply shaded stations, or in open localities far removed from vegetation. This problem has not, however, been studied statistically. As has been noted, in the two shadiest, muddiest collecting areas the spoon-tipped hairs were relatively poorly developed.

*Material:* A total of 645 specimens was taken near the mouth of the San Juan River 8 miles above the bar (Cat. no. 42168), at the mouth of the Caño Manamo (at Pedernales, Cotorra Island and Tapure, Cat. no. 42420), and from Maracaibo, from five col-



lecting stations between the Yacht Club and a point three or four miles to the north (Cat. nos. 42,421, 42422, 42426, 42427).

*Uca cumulanta* sp. nov.

Pl. I, Figs. 4-6; Text-figs. 1G,H,I.

*Diagnosis:* Carapace strongly convex, but not quite semi-cylindrical in lateral view; front behind eyes a little more than a fifth maximum width of carapace; orbits little oblique; antero-lateral margins well developed, straight or slanting slightly outward (rarely inward); then continuing backward and inward with an angular turn; orbital angle usually a right angle, sometimes slightly produced; minor chelae strongly serrated in middle three-fifths; gape slight; hairs on chelae moderately plentiful. Oblique tuberculated ridge inside major palm present, continued to upper margin and strong throughout, with the single row of tubercles splaying out distally into a small irregular patch. Pollex moderately slender with a small, serrated elevation halfway to its tip, and usually one or more enlarged teeth distal to this. Merus of second maxilliped with not more than 25 spoon-tipped hairs. Merus of ambulatories moderately enlarged in male and female. Small patches of pile, inconstant in amount and location, present on carapace. Arm on abdominal appendage of male short but well developed. Eyebrow broad, little inclined.

*Description:* A small species. Carapace with H-form depression distinct, but regions otherwise poorly defined, naked except for small patches of scanty pile present in any or all of following locations: in upper half of H-upright (most constant and plentiful here), in entire H-form depression, in depression between hepatic, orbital and antero-lateral margins, and in mid-branchial depressions. In addition there are a few widely scattered microscopic hairs in carapace surface.

Carapace strongly convex, but not semi-cylindrical in lateral view, widest usually behind orbital margins. Latter are well developed, straight, usually slanting a little outward, rarely faintly inward, about four-fifths as long as width of front behind eyes. They then turn inward and backward at an angle, continuing in the form of the usual ridge as far as middle of cardiac region. Sides of carapace slightly concave, little converging. Front between posterior margins of eyestalks about a fifth width of carapace, its margin visible in dorsal view. Upper margin of orbit sinuous, scarcely oblique. Eyebrow broad, equal in width to adjacent portion of eyestalk, little inclined. Lower orbital margin moderately projecting with crenulations weak internally, strong externally. Suborbital region naked except for a

row of hairs immediately behind orbital margin. All abdominal segments distinct.

Spoon-tipped hairs on merus of second maxilliped few, about 15 to 25 or less, poorly developed. Woolly hairs moderately plentiful. Ischium of third maxilliped with central grooves represented only by a marginal depression.

Minor chelae about one and one-fifth times longer than palm, with strong serrations throughout middle three-fifths; distal fifth corneous, slightly dilated, the tips articulating well. Gape very slight. An oblique row of long, soft hairs (longest distally as usual), and a straight row of wide-set short hairs on inner surface of each chela; two rows of short hairs, most set in series of three on their external surfaces, and two other similar rows along dorsal profile of dactyl and ventral of pollex respectively.

Major cheliped of male with arm only slightly rugose except on upper distal surface, wrists somewhat rougher. Both furnished externally with small, variable amounts of pile. Hand at most about four-fifths as broad as long. Upper surface rounded, except for a slightly elevated double line of fine granules; lower margin with a single line of similar ones; upper and outer surfaces with low, small tubercles; lower practically smooth.

Inner surface of major palm with pile on proximal articulating surface of carpal cavity. A strong oblique tuberculated ridge arising some distance proximal to base of pollex, proceeding obliquely up and back to carpal cavity, then following margin of latter almost to dorsal profile. Tubercles of uppermost portion, although large and strongly developed, splay out into an irregular double or triple formation. Carpal eminence well developed. A row of tubercles extends from proximal tenth of pollex, close to upper margin, obliquely back and up along distal part of manus, where the tubercles are large and close-set, the last tubercles approaching uppermost ones of main oblique ridge. Distal to this, paralleling base of dactyl, is a row of about five, smaller, close-set tubercles.

Major dactyl about one and a third times as long as palm, moderately convex, curving down beyond tip of pollex. Pollex slender, not triangular, with a small serrated elevation, of which distal tooth is enlarged, halfway to its tip, and at least one considerably enlarged tooth distal to this. The dactyl has only one tooth strikingly enlarged, located at about middle of its length. Gape wide. A row of close-set tubercles arising on outer side of distal end of manus continues out along upper surface of pollex, close to prehensile margin, to its tip. A corresponding row is traceable almost the entire length of the dactyl.

Merus of ambulatories moderately en-

larged in both sexes, that of third ambulatory in male usually extending scarcely beyond antero-lateral margin when laid forward. Pile on ambulatories practically lacking.

Abdominal appendage of male slender, curving, tapering. Subterminal arm short but well developed, arising at beginning of distal seventh of appendage. Genital opening of female set in a depression, without marginal tubercle.

*Measurements:* Male holotype, length 8.4 mm., breadth 13.9 mm., base of manus to tip of pollex 24.5 mm.; seven male paratypes, length 6.3 to 7.8 mm.; six female paratypes, length 6.9 to 8.4 mm.; smallest male, length 4.4 mm.; smallest female, length 4.8 mm.; 29 additional males and 19 additional females of intermediate lengths.

*Color:* Displaying males observed through binoculars: carapace (rarely free of mud except anteriorly) iridescent green, marbled and mottled at least posteriorly with dark brownish and grayish-white. Major cheliped dull grayish or brown except chelae: dactyl has rosy tinge on upper basal part; both chelae otherwise white or yellowish except for extreme tips which may be pale peach, or the fingers may be apricot at base, white distally. Legs grayish, banded light and dark. Females dull brownish.

*Display:* This is a simple beckoning routine which starts with the crab moderately elevated and with the cheliped flexed in front of the mouth and held clear of ground. Display is of moderate speed, at the rate of about one to the second, but with a long pause, of two seconds or more, between displays in the same series, except when the crab is waving with especial vigor, usually when the attention of a female has been attracted. Then, at the end of most of the beckonings or wavings, several vibrations pass along the major cheliped, the muscular movement taking place in the merus and above. The ground is not actually touched with the manus and pollex, as in other species of this rapper group, except at moments of the greatest excitement. One male was seen to reach the stroking stage of courtship with two females in quick succession, each of which rejected him and escaped. Finally still another female did follow a second male into his hole. Neither of these males had a shelter (see next paragraph). When I first saw the apparently successful male, the female was two inches away and watching him; he was finishing a routine display; as the female started toward him, he went halfway down his hole, rapping the manus and carpus of the major cheliped three or four times hard against the hole's edge, then vanished. The female came over at once, looked down, then went two inches beyond the far side of hole, and waited. In

about a minute the male reemerged, looked around, dashed straight to the top of a small mound two inches from the opposite side of the hole from the female, and displayed vigorously, with rapping, just once. Thereupon the female suddenly dashed down his hole and he ran back and followed her down at once. Since the tide was coming in rapidly and I needed the crabs for identification, I secured them after another five minutes. A similar procedure was observed between a male with a well-built shelter and another female. One crab—and only one—was seen again and again to climb upon his shelter to display.

*Shelter:* As with shelter-builders of Group 5 observed in Panama, it was found that only displaying males, but not all of these, built shelters. In this species the shelter, although in general form a half-dome as in Group 5, is roughly made, very variable, and always exceedingly thick with a relatively small entrance hole, just large enough to receive the crab. A typical one measured an inch and a half in height and was slightly wider, outside dimensions. On the whole, these shelters bear far more resemblance to the shelters of Group 5 crabs than to the structures of *U. minax* (Group 2). About half the displaying males had shelters.

*Breeding:* No ovigerous females were seen or taken in late August when the collection was made, although the males showed more display activity than did those of the other species.

*Affinities:* This crab seems to be most closely allied to *coloradensis*, known only from near the head of the Gulf of California. The new form differs from this species in having the front only about two-thirds as wide, a stronger oblique ridge on the inner surface of the major palm, with the individual tubercles rounder and more isolated, and with the two tuberculated ridges at base of dactyl moderately divergent, instead of parallel. Both in its physical characteristics and in the rapping form of its display, this crab belongs clearly in the series I have designated (1941, p. 166) as Group 4. As in *coloradensis*, however, the relatively high development of the spoon-tipped hairs on the merus of the second maxilliped, of the arm of the abdominal appendage, and of the teeth on the suborbital margin, as well as the less rounded carapace and less specialized pollex of the major cheliped, all show that the proposed new species is a primitive member of its group, compared with the end forms, *batuenta* and *saltitanta*. The display, with the rapping phase occurring only at moments of excitement, instead of throughout display, is also primitive in character; unfortunately I have as yet had no opportunity of observing the display of *coloradensis*; the comparison should prove interest-

ing. This new species is the first of its group which has been observed to build a shelter, and the first time a member of the group has been reported from the Atlantic coast. The building of the primitive shelter may perhaps indicate the basic, ancestral affinities of this group with the typical shelter-builders—*beebei*, *latimanus* and *terpsichores*—of Group 5.

*Range:* Known only from Pedernales, Venezuela.

*Local Distribution:* The 64 specimens were found on several sandy-mud or muddy beaches in the immediate vicinity of Pedernales (i.e., from the beach at Pedernales itself, from Tapure, and from the shore of Cotorra Island), always completely in the open, but fairly near mangroves.

*Material:* Male holotype; Cat. no. 42423, Pedernales, Venezuela; 7 males and 6 female paratypes, same locality; Cat. no. 42424; 38 additional males and 26 additional females, same locality, Cat. no. 42425.

The name *cumulanta* is given in reference to this crab's habit of heaping up mud.

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#### EXPLANATION OF THE PLATE.

##### PLATE I.

- Fig. 1. *Uca murifecenta*. Male holotype (Cat. No. 42167), dorsal view. Carapace length 14.5 mm.
- Fig. 2. *Uca murifecenta*. Major chela of holotype, inner view.  $\times 2.4$ .
- Fig. 3. *Uca cumulanta*. Male holotype (Cat. No. 42423), dorsal view. Carapace length 8.4 mm.
- Fig. 4. *Uca cumulanta*. Major chela of holotype, inner view.  $\times 4.3$ .





FIG. 1.



FIG. 2.



FIG. 3.



FIG. 4.

CRABS OF THE GENUS UCA FROM VENEZUELA.



## 8.

Observations on the Electric Discharge of *Narcine brasiliensis* (Ölfers).

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Text-figures 1-4.

*Narcine brasiliensis* (Ölfers), in common with other members of the order Narcacnites, shows marked electric power, as has been often noted. It gives a severe enough shock that fishermen, when they net it, avoid handling it alive, and Coles (1910) has reported being knocked down by its discharge. The utility of this power in the normal environment of the fish has not been studied. Its protective value would seem to be obvious, but if there are more subtle uses they await further investigation.

Heretofore observations on the electrical activity of this species have been made under rather fortuitous circumstances and the information given has been of necessity somewhat fragmentary, Bean & Weed (1911) and Breder & Springer (1940). In the hope of being able to make a more systematic study, the present work was undertaken in June, 1941, at the laboratory of the New York Aquarium at Palmetto Key, Florida. Electrical measurements were made on twenty live specimens, including fourteen adults, with both sexes represented, and six prematurely born young, belonging to two litters. These were born nearly at full term, with a small dependent yolk sac. A specimen from the first litter was observed about a quarter hour after birth. One from the other litter was some hours old at the time of the first observation. Electrical measurements were made on the mother of one litter just before birth and on the mother of the other litter within a day after birth. Thus the range of variation in the condition of the specimens included the chief phases in the life of the fish.

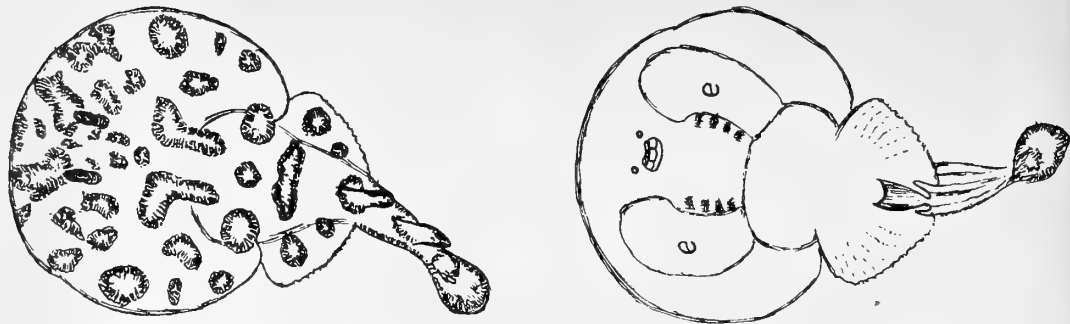
The discharge is produced by paired electric organs, similar to those described for the related and better known genus, *Torpedo*. They comprise in *Narcine* about one-

sixth of the weight of the fish, which is roughly the same as the proportion found in *Torpedo occidentalis* but much less than that in *Electrophorus electricus*, where half the weight of the fish is in the electric organs. It has been remarked by Coates, Cox & Granath (1937) that the shape of the organs in the principal electric species is suited to produce a maximum output of power in the water they inhabit, whether fresh or salt. Thus the chief marine species have organs with their greater dimensions transverse to the axis of electric polarity, in contrast to the fresh water species, in which the organs are elongated parallel to this axis. An earlier similar observation was made by du Bois-Reymond, as noted by Gotch (1900). *Narcine* accords with this principle. The electric poles of the organs are their dorsal and ventral surfaces, and the smallest diameter of these surfaces is still several times larger than the average distance between them. The dorsal surface is positive, as in *Torpedo*. The polar surfaces are covered only by thin layers of connective tissue and skin. The outline of the organs is clearly visible on the ventral surface and visible also, though somewhat obscured by the spots in the skin, on the dorsal surface. (See Text-fig. 1.) The thickness of the organs decreases toward the periphery of the body from their inner edge, which is at the line of the gill slits.

In *Narcine*, as in *Torpedo*, the electric organs resemble honeycombs in their structure, the electroplaxes lying in piles of roughly prismatic shape, which extend from dorsal to ventral surface. Blood vessels supplying the electric organs lie in the sheaths of connective tissue which separate the prisms of electroplaxes.

The number of prisms of electroplaxes was counted in several specimens, and the counts are given in Table I. The count

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Text-fig. 1. Embryo *Narcine brasiliensis* (Ölfers). Dorsal and ventral views. "e" — electric organs. Yolk attachment omitted. Width of disc = 48 mm.

could in no case be made with precision, and in one of the embryo specimens the condition of the material caused a very large uncertainty. All counts refer to a single organ of the pair.

bryos, their organs being small enough for adequate penetration. With these specimens counts were obtained as shown in Table II. Sections prepared from two adult specimens, #5 and #10 in Table I, were only clear

TABLE I.  
Number of prisms of electroplaxes in one organ of various specimens.

Specimen	Counts	Average	
#5, adult male	356, 343	350	
#10, adult female	376, 388	382	
another adult	402, 416	409	Average for three adults, 380
#E5, embryo	267, 267	267	
another embryo	290, 340	315	
another embryo	264, 287	276	Average for three embryos, 286

It will be noticed that the lowest count for an adult is higher than the highest for an embryo, and the average of the embryos is only three-quarters that of the adults. If anything could be inferred from counts on so few specimens, it would be that the number of prisms increases during the growth of the fish, but much the more important factor in the growth is the increase by approximately nine-fold in the average area of cross-section of the prisms.

Counts were also made of the number of electroplaxes in one prism. Formalin was used as a fixative and is evidently not very satisfactory for this purpose. Fairly clear sections were obtained from two of the em-

enough for rough guesses of the number of electroplaxes in series. The electroplax boundaries were badly broken and displaced and the nuclei, the rows of which were found to be useful features for counting electroplaxes in the smaller organs, were not distinct in these. Such estimates as could be made gave no evidence of an increase in the number of electroplaxes in a prism during the growth of the fish after birth. The mean of two rough estimates of the number of electroplaxes in prisms of the two adult specimens was actually somewhat less than the mean of the counts from homologous prisms of the embryos.

In the development of the eye, *Narcine*

TABLE II.  
Number of electroplaxes in one prism of the organs of various specimens.

Specimen	Position of prism in organ	Counts	Average
#E5, embryo	short prism near outer edge	180, 178	179
	long prism near inner edge	314, 296	305
	short prism near outer edge	321, 273, 270, 288	288
#E4, embryo	long prism near inner edge	483, 481	482

presents a contrast with *Electrophorus*. The eyes of *Electrophorus* deteriorate with increasing age, and it has been supposed by Coates, Cox & Granath (1937) that the deterioration is an injury produced by the electric discharge. The eyes of *Narcine*, like those of some other marine electric species, are very near the electric organs, but they do not seem to be inferior to the eyes of other rays. It seems reasonable to suppose that some difference in the two species or in the electrical characteristics of the waters they inhabit might make the electric discharge injurious to the eye of one but not to the eye of the other. If so, an understanding of this difference would be of interest.

The first two specimens of *Narcine* obtained alive in the present work sustained an injury to the eye of a quite different sort from that just considered but of some interest in another connection. These specimens were left in a "live car" from which a miscellaneous collection of fishes had been removed. Those remaining, besides the two *Narcine*, were three flounders, *Paralichthys albiguttus* (Jordan & Gilbert), and, by inadvertence, two pin fish, *Lagodon rhomboides* (Linnaeus), overlooked because of their small size. The first intimation we had of the presence of the pin fish was that the next day both *Narcine* were without eyes. It is well known that the pin fish, along with other species, has a tendency to pick at the eyes of fish which lie prone on the bottom, attracted apparently by the movement and brightness of the eyes. Inasmuch as the unprotected flounders were not injured, it was distinctly surprising to find that in spite of their electric power the *Narcine* were unable to protect themselves. It may be that they soon exhausted their ability to discharge electricity, as they apparently do, and then in confinement were at a disadvantage, since they are notably less alert than the flounders. Another consideration is that *Narcine* is seemingly reluctant to discharge. Certainly such injury to the eye would be expected to call forth all protective measures, but perhaps the injury was inflicted before the electric discharge could be produced.

The discharge is generally accompanied by muscular activity similar to that described by Coates & Cox (1942) in *Torpedo occidentalis* and much more pronounced than the slight tremor which is sometimes seen to accompany the discharge of *Electrophorus*. This activity, it was observed, varied somewhat from fish to fish and from one time to another, but it tended to follow a fairly regular sequence. When about to discharge the fish usually turns up the edges of the pectorals, so as to form an upstanding frilled edge. Next there follow muscular con-

tractions running down the back and, at the moment of discharge, an almost tetanus-like quiver goes through the whole fish. This series of events may or may not be accompanied by swimming movements of more or less vigor. Usually if these occur they start at about the time of discharge and can be taken to indicate that more discharges will follow quickly. After the effort is over, the fish lies quiescent and does not repeat either electrical or muscular activity for some little time. After several efforts of this kind the fish gradually becomes limp and flaccid and requires a considerable period of rest before more discharges can be elicited.

The observations just described were made along with the electrical measurements. To make these measurements the fish was removed from the water and laid on an aluminum plate which thus made electrical connection through the wet skin of the fish with the ventral or negative poles of the electric organs. A smaller aluminum plate covered and made connection with the dorsal or positive surface of the organ on one side, right or left. The two plates were joined by wires to the terminals of a cathode ray oscillograph, which could thus be used to measure the voltage developed between the two poles of the organ. One of us manipulated the fish while the other made the electrical measurements. A close check on the association of the muscular and electrical activities of the fish could be made by the manipulator of the fish alone, whether or not he observed the oscillographic screen, because he could practically always feel the shock of the discharge in the hand with which he held the fish and the upper electrode in place. The hand was protected by a rubber glove, but the dampness of its surfaces, inside from perspiration and outside from the fish, permitted a distinctly appreciable current to pass. In fact it was necessary to keep two pairs of gloves in service, one drying while the other was in use, to prevent the passage of a cramping current. The sequence of muscular and electrical activity was regular enough that the manipulator of the fish could generally foretell a few moments in advance that the discharge would be produced, a feature of some convenience in the observations.

The exact significance of these muscular movements is not clear. Possibly the strong quiver at the instant of the discharge is evidence that the fish receives some shock from its own current. The tremor sometimes seen in *Electrophorus* also occurs at the instant of discharge and would seem thus to be the counterpart of this phase in the muscular sequence of *Narcine*. In *Electrophorus* the quiver can be intensified locally by the use of small electrodes concentrating the cur-

rent in a chosen region, and it thus appears to be simply the muscular contraction caused by shock. Therefore the intense quiver in *Narcine* may also have this explanation.

For the sequence as a whole, the most likely interpretation would seem to be that its various phases are the different parts of an effort to escape. The curling and frilling movements appear to be an exaggeration of those used to flurry sand over the back, a habit common to most rays, which in a state of nature serves to blanket them from vision. This failing, an electric discharge should protect, but finally, this also failing, flight, as shown in the swimming movements of the muscular sequence, would be resorted to as in most animals when the special defense reactions do not produce the customary result.

These fish do not give off their discharge readily at best, and at no time in netting them from the live car in which they were kept were they noted to do so. In fact after a time it was found that they could be transferred by the bare hands without danger of a shock. When they were in place for the observations, it was usually necessary to prod, lightly pinch, or otherwise annoy them in order to elicit the desired discharge. Various methods were tried in order to obtain a quick and sure stimulus. These included pinching the caudal fin, stroking the back, bending the tail and others. Each seemed to give promise when first tried but soon failed, and it finally developed that a new stimulus was more effective than any one kind often repeated. After the fish had discharged several times, it would sometimes carry through the pattern of muscular activity which normally precedes the discharge, but without discharging.

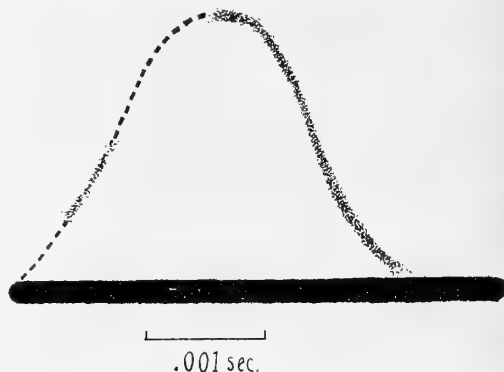
The electric organs of *Narcine*, like those of other electric species, discharge intermittently in brief pulses, which follow one another to form a train of variable length. One or a few such trains constitutes the discharge associated with the muscular sequence which has been described. A faint photograph of the oscillographic traces of such a train, showing the regularity of the peak voltages and of the interval between



Text-fig. 2. Oscillographic trace showing the train of pulses in the discharge.

pulses, is copied in Text-fig. 2. (Only faint photographic traces were obtained because the power supply was not quite enough for the oscillograph.) The train shown is typical insofar as there is a type, but wide variations were noticed. The first of the young fish to be observed, about 15 minutes after a premature birth, gave from two to five pulses at irregular intervals in a train. The young of the second litter, also premature but some hours old at the time of observation, gave discharges in better formed trains of about five pulses to the train. There were more pulses still in the trains produced by adults, and the interval was regular enough that when the discharge passed directly through a telephone receiver it produced a short but clear musical note. One specimen, a gravid female, gave trains of one hundred or more pulses, as well as the eye could reckon them, but this behavior was exceptional.

Text-fig. 3 shows the form of a single pulse on a more open time scale than that of Text-fig. 2. This figure also is drawn from a faint photograph, but the dotted portion is supplied from memory of visual observation. The trace was obtained with the electric organ as nearly as possible on "open circuit," no significant current being drawn except that which flowed in the circuit made through the body of the fish. A comparison of this trace with those obtained similarly by Coates & Cox (1942) from *Torpedo occidentalis* and *Electrophorus electricus* shows that the pulse form of *Narcine* resembles that of *Torpedo* rather than that of *Electrophorus*, as might be expected on a basis both of relationship and of structural detail.



Text-fig. 3. Oscillographic trace of a single pulse.

The synchronization of the discharge in the two electric organs of one fish was tested by the method Coates & Cox (1942) employed with *Torpedo*. One organ was connected, instead of the timing circuit, to the oscillograph to produce the horizontal mo-

tion of the electron beam, while the other organ caused the vertical motion as usual. If the two organs discharge in exact synchronism, the resulting trace is a straight line; otherwise it is a loop the width of which shows the time lag between the pulses in the two organs. One newborn specimen and several adults were observed in this way. Observations of the same kind, but with small electrodes each covering only a part of the organ on one side, were also made in order to see if the pulse were simultaneous in all parts of the same organ. The result of all these observations was to show that all parts of both organs discharge in almost exact synchronism. Occasionally the synchronization was not quite perfect and the pulse from one organ followed that from the other by about .0001 second, or one thirtieth the duration of the pulse. Even these deviations were more frequently observed after the fish had discharged a number of times, and they may therefore be signs of fatigue.

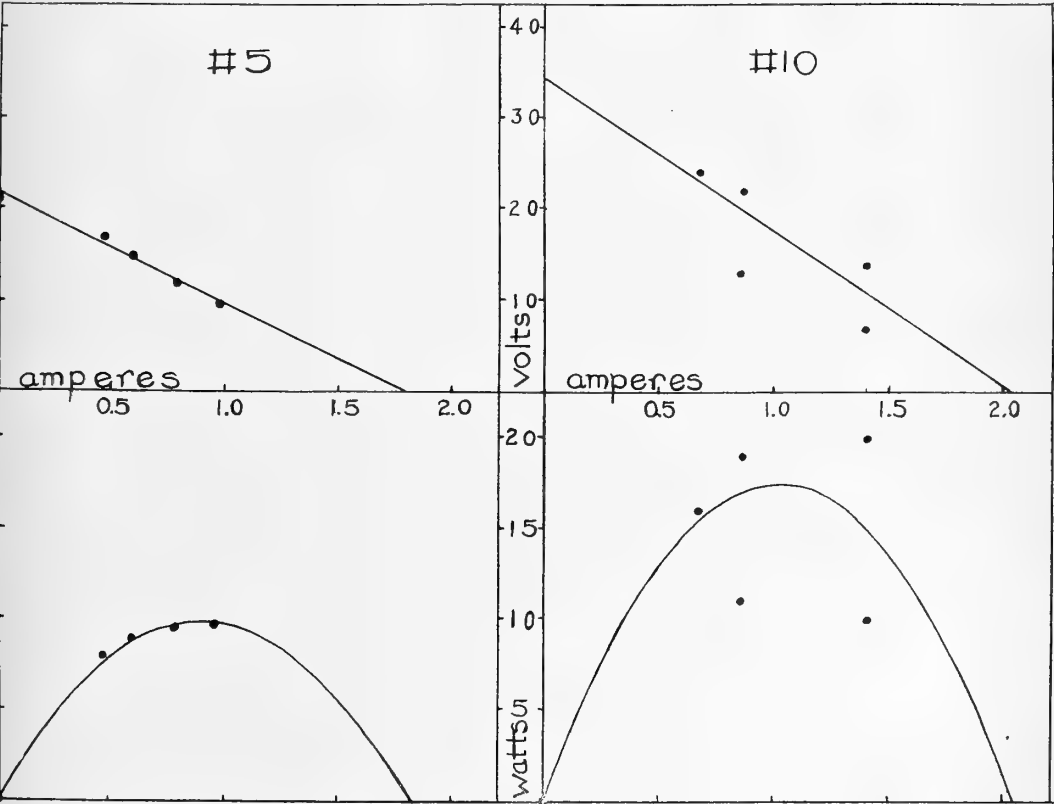
Many measurements were made, visually with the oscillograph, of the peak voltages of the pulses produced by the various

specimens. Voltages were measured both on open circuit and when current was drawn from the organ through known external resistances. The voltage being  $V$  and the resistance  $R$ , the current  $I$  flowing in the external resistance is given by  $I = V/R$ , and the power  $P$  by  $P = VI$ . These measurements and computations are shown for two specimens in Table III.

TABLE III.  
Voltage, current and power at peak of discharge for various values of external resistance.

Specimen	R ohms	V volts	I amperes	P watts
#5	$\infty$ *	21	0	0
	35.8	17	0.47	8.0
	25.5	15	0.59	8.9
	15.3	12	0.78	9.4
	10.3	10	0.97	9.7
#10	$\infty$ *	37	0	0
	35.8	24	0.67	16
	25.5	22	0.86	19
	15.3	13	0.85	11
	10.3	14	1.4	20
	5.0	7	1.4	10

\* Open circuit.



Text-fig. 4. Graphs of voltage and power against current, all at the peak of the discharge.

These data are plotted in Text-fig. 4. It will be seen that the graph of voltage against current is quite near to a straight line with specimen #5. With specimen #10 the points scatter widely and no smooth graph could be drawn to pass near all of them. These two fish gave, respectively, the most consistent and the most erratic data obtained. In general we find, not only with *Narcine*, but also with *Electrophorus* and (though with fewer observations) with *Torpedo*, that the more we can avoid tiring the fish the more nearly the plotted values of voltage and current determine a straight line.

The maximum voltage of the organ is produced when the external current is zero, and it is thus the intercept of the plotted line on the axis of voltage. If there were no circuit made through the body of the fish, so that the internal current was zero as well as the external current, then the maximum voltage would be equal to the electromotive force of the organ. It seems likely that the electromotive force is actually not much greater than the maximum voltage.

The two graphs in the lower half of Text-fig. 4 show the power delivered to the external circuit for different values of the current. These graphs are plotted by the equation  $P = VI$  from the values of  $V$  and  $I$  taken from the graphs above. The plotted points are those from Table III computed by the same equation. The power is maximum when the voltage and current have half their maximum values.

Table IV summarizes the results obtained with the whole group of adult specimens by the methods illustrated with specimens #5 and #10. The values of maximum power given in this table are reckoned for both organs discharging together. Thus the values given for specimens #5 and #10 are twice those shown in Text-fig. 4.

As is also true with *Torpedo*, the electromotive force and power of the electric organs of *Narcine* decline rapidly as the physical condition of the fish is impaired by fatigue or other causes. For this reason the maximum values of voltage and power shown in Table IV may be more characteristic of the normal specimen than the average values are.

The observations obtained with the newborn specimens were much less complete. The peak voltage of one of the first litter was measured and found to be 6 volts. The voltage was so much lowered by connection to even the highest of our measured resistances that the maximum power was not accurately measured. It was estimated as about 0.1 watt for the two organs of this fish discharging together.

The second litter was born in a tank in which the mother was being brought to the laboratory. Measurements of the voltage on open circuit were made promptly. One fish showed a peak voltage around 22 volts, three between 13 and 16 volts, and one around 3 volts. This last was pale in color, a sign of poor condition, and it died within a few hours. Measurements were repeated on three of the fish, and the voltages were found somewhat lower on the average than at first. No determination of the power was made. The highest voltage measured with one of these newborn fish, 22 volts, being almost equal to the average for the adults, it seems that the electromotive force of the organ does not increase proportionately, if it increases at all, with the growth of the fish. It has already been noted that the number of electroplaxes in series does not increase proportionately with growth and may, as far as we can tell, be fixed at birth.

The number of electroplaxes is not well known, however, for any of our adult speci-

TABLE IV.

Dimensions, weight, peak voltage on open circuit and maximum power of various specimens.

Specimen	Sex	Length cm.	Width cm.	Weight gm.	Peak voltage, open circuit volts	Maximum power watts
1	m	25	13	—	18	—
3	m	24	12	230	15	7
4	f, gravid	32	17	450	23	—
5	m	26	13	250	21	19
6	m	28	14	300	29	19
7	f	25	14	270	21	11
9	m	26	13	210	25	16
10	f	27	14	280	37	35
11	f	26	14	270	14	5
12	f, gravid	33	18	650	27	25
average	m	26	13	248	22	15
"	f	29	15	gravid, 550 others, 273	24	19
"	m and f	28	14		23	17



mens. It is impossible therefore to determine with any accuracy the electromotive force per electroplax. Probably the right order of magnitude will be found by taking 30 volts as the electromotive force of 300 electroplaxes in series, which gives 100 millivolts as the electromotive force per electroplax. Values on both sides of this are observed in *Electrophorus*.

The weights of the electric organs and their cross-sectional areas perpendicular to the direction of the current, parallel, that is, to the dorsal and ventral surfaces, were measured for specimens #5 and #10. From these and the electrical measurements already given we find the maximum power delivered externally per gram of tissue and the current per square centimeter flowing through the tissue at maximum power.

These values are in Table V below. Those reported for *Torpedo occidentalis* are given for comparison. In each case, the weight, power and current are those of both electric organs.

cording to the condition of the fish. The electric power is well developed at birth.

The two organs discharge simultaneously in a train of pulses in rapid succession. Each pulse lasts about .003 sec., and the number in one train varies from about five to (exceptionally) one hundred or more. The discharge is accompanied by a muscular sequence which appears to be made up of motions of concealment and flight and perhaps self-shock. The power released externally attains in the discharge an instantaneous value of about 0.7 watt per gram. The current density in the organ when this power is developed is about .05 ampere per sq. cm.

Comparison with other electric fish shows electrical resemblances between *Narcine* and *Torpedo* as marked as their morphological resemblances. The electrical differences are only those to be expected from the difference in size. Also, in every respect in which one of these fishes shows a difference in electrical characteristics from *Electrophorus*, the other shows a difference of the same sort.

Table V.  
Specific current and power of *Narcine* and *Torpedo*.

Specimen	Total weight gm.	Weight of electric organs gm.	Fraction of weight in electric organs	Maximum power watts	Maximum power per gm.	Current at maximum power amperes	Cross-sectional area of organs sq. cm.	Current per sq. cm.
<i>Narcine</i>								
#5	250	42	0.17	19	0.5	1.8	44	0.04
#10	280	52	0.19	35	0.7	2.1	41	0.05
<i>Torpedo</i>	25,000	4,000	0.16	6,000	1.5	60	500	0.12

We wish to express our thanks to the Department of Biology of New York University at University Heights for technical assistance in the preparation of sections of the electric tissue.

SUMMARY.

The adult *Narcine brasiliensis* used in this study has an average length of 28 cm., an average width of 14 cm., and an average weight around 270 grams, the female being slightly larger than the male. About one-sixth of its weight is in two electric organs, which extend from dorsal to ventral skin, the dorsal surface being the positive pole. Each organ is a parallel array of 300 to 400 prisms of electroplaxes, with something like 300 electroplaxes in series in one prism. The growth of the organ is more an enlargement of the electroplaxes than an increase in their number; neither the number of prisms nor the number of electroplaxes in one prism increases greatly after birth. The electromotive force per electroplax is of the order of 100 millivolts but varies widely ac-

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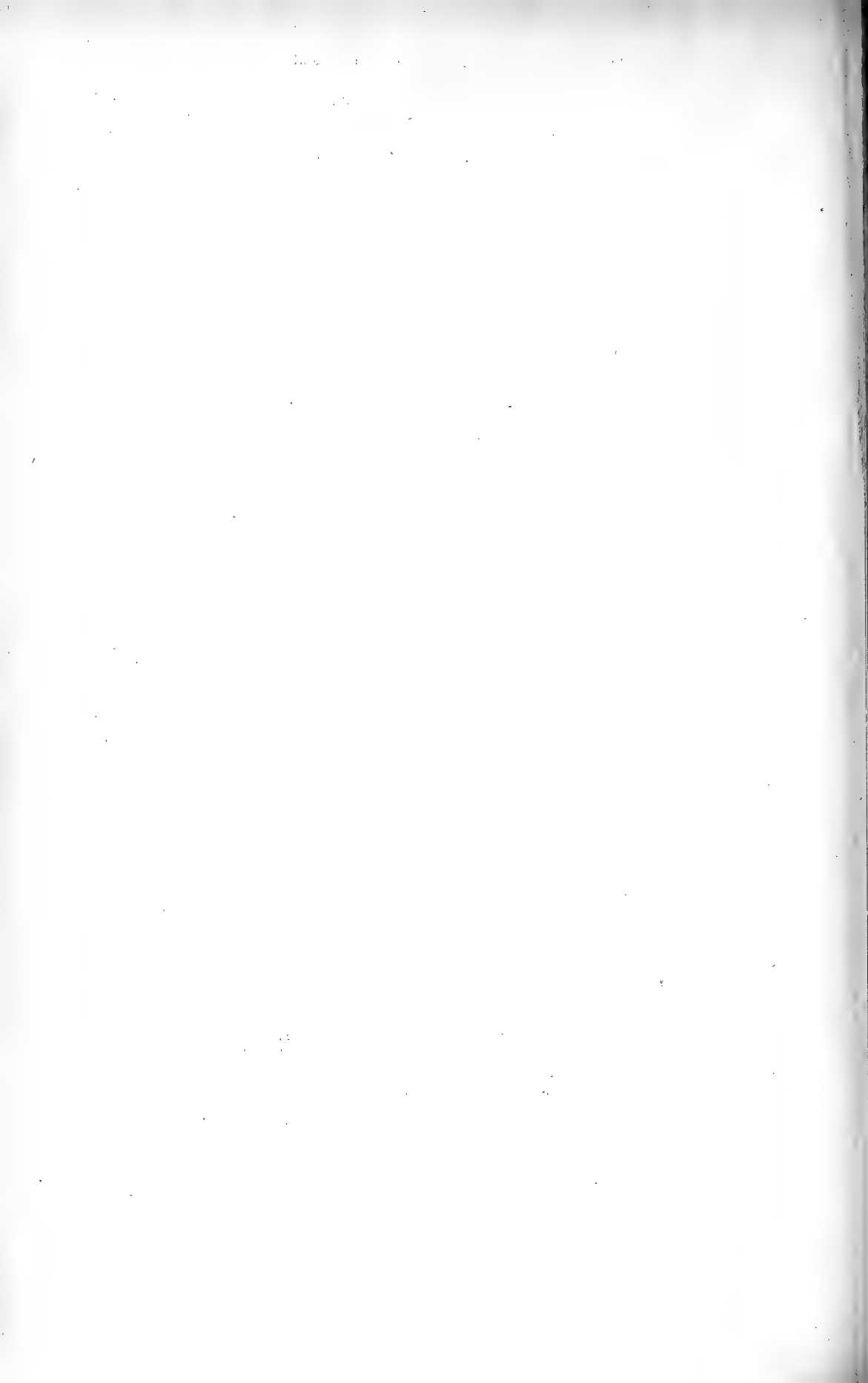
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## 9.

Physical Factors in the Ecology of Caripito, Venezuela.<sup>1</sup>

WILLIAM BEEBE

*Department of Tropical Research,  
New York Zoological Society.*

(Plates I &amp; II; Text-figures 1-5).

## INTRODUCTION.

The Forty-third Expedition of the Department of Tropical Research of the New York Zoological Society had its headquarters at Caripito, in northeastern Venezuela. Under the direction of Dr. William Beebe the expedition left New York for Venezuela on February 12, 1942, and returned on September 20, flying both ways on Pan American planes. The elaborate outfit made a safe transit by sea on the Standard Oil tanker *Aruba*. The members of the staff were Jocelyn Crane, Research Zoologist; George Swanson, Artist; Henry Fleming, Entomologist; and Mary Vander Pyl, Associate.

Invaluable assistance and support were given by a grant from the Committee for Inter-American Artistic and Intellectual Relations, by the Standard Oil Companies of New Jersey and Venezuela, and by four Trustees of the Zoological Society, Laurance Rockefeller, Childs Frick, Herbert L. Satterlee and George C. Clark.

Field work was carried on in the jungles about Caripito from February 19 to September 2. The objects were to make life history and ecological studies, to secure extensive color motion picture records of wild life, to record the reactions of animals to the very distinct dry and wet seasons, and to make detailed observations through high power binoculars of 12, 20 and 40 diameters.<sup>2</sup>

Five lectures with motion pictures were given in Caracas and Caripito, and constant, constructive relationships were initiated and maintained with Venezuelan scientists and institutions.

The object of the following brief ecological survey of this area is to afford a background for forthcoming zoological studies and also offers direct comparison with the environment of Kartabo, British Guiana,

528 kilometres (330 miles) to the southeast. Under typical tropical rain forest conditions we have devoted, in the past, eight expeditions to researches in the vicinity of Kartabo.

There is very little in literature concerning the ecology of the Caripito area, and until I arrived I had expected the general conditions to approximate those at Kartabo, about the same distance away as Buffalo is from New York City. I was completely mistaken, and found, as will be seen, that Caripito possesses a curious admixture of several distinct floral and faunal zones, all of them quite atypical of a true tropical rain forest.

For direct comparison with the ecological conditions existing at Kartabo, refer to Beebe, "Studies of a Tropical Jungle," *Zoologica*, VI, 1, 1925, pp. 1-193.

## GEOGRAPHICAL POSITION.

Caripito is situated in northeastern Venezuela in the extreme north of the State of Monagas, in 10°09' N. Lat., and 63°05' W. Long. The following distance lines of radiation will serve to complete its orientation:

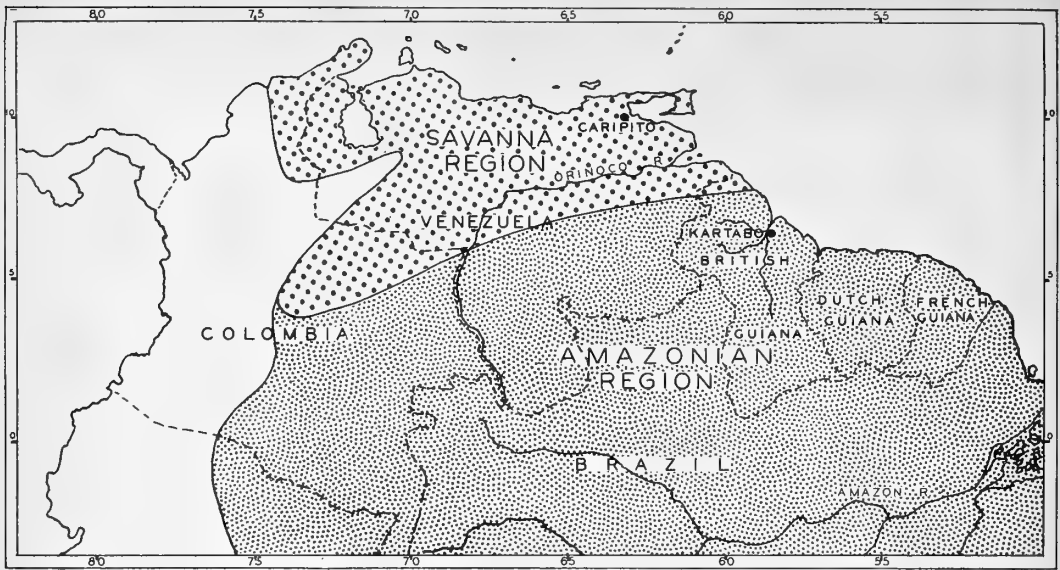
	Kilos.	Miles
North to Caribbean Sea	67	42
Northeast to Port-of-Spain	182	114
East to Gulf of Paria	50	31
Southeast to Kartabo,		
British Guiana	528	330
South to Quiriquire (by road)	27	17
South to Maturin (by road)	43	27
South to Ciudad Bolivar		
& Orinoco River	223	140
West to Caracas	434	271
Northwest to Cumaná	127	80
Northwest to New York	3570	2233

## GEOLOGY.

A geological map of northeastern Venezuela shows Caripito at the very edge of two very unlike formations. To the west and north are hills and mountains; solid outcroppings of Upper and Lower Cretaceous

<sup>1</sup> Contribution No. 665, Department of Tropical Research, New York Zoological Society.

<sup>2</sup> Two contributions have already appeared: Beebe, W., "Pattern and Color in the Cichlid Fish, *Aequidens tetramerus*," *Zoologica*, XXVIII, 3, 1943, pp. 13-16; Crane, J., "Crabs of the Genus *Uca* from Venezuela," *Zoologica*, XXVIII, 7, 1943, pp. 33-44.



Text-fig. 1. Faunal regions of northern South America. (After Cabrera and Yepes).

series of grits, limestones and shales. Away from the foothills, to the south, the Pleistocene and Recent alluvial deposits of the llanos clays, sands and gravels become dominant. These last formations are characteristic of immense extents of territory bounded by the Orinoco Delta on the east and hundreds of miles of the Orinoco River itself, as well as extending varying distances to the south of this river in the direction of the British Guiana boundary.

According to Schuchert (1935, "Historical Geology of the Antillean-Caribbean Region") Caripito has been submerged a number of times: in the Middle Pennsylvanian, Middle and Upper Cretaceous, and throughout the Eocene, Oligocene, Miocene, Pliocene and Pleistocene.

#### FAUNAL REGIONS.

The most recent as well as the most generalized segregation of faunal regions in northeastern South America is that in "*Mamíferos Sud-Americanos*," published in Argentina by Dr. Angel Cabrera and Dr. José Yepes. In the colored *Mapa de los Distritos Zoogeográficos de América del Sur* they show the arrangement which is presented in Text-figure 1. Almost all of central and northern Venezuela as well as corresponding portions of Colombia are designated as the Savanna Region (*Distrito Sabánico*), whereas all the territory of Venezuela well south of the Orinoco, the Guianas and a considerable part of Brazil, are included in the Amazonian Region (*Distrito Amazonica*).

Future definite and detailed studies of organisms of this region will enable us to

elaborate and delimit more accurately these faunal zones.

#### PHYSICAL GEOGRAPHY.

(Text-fig. 2; Pl. I; Pl. II, Fig. 3).

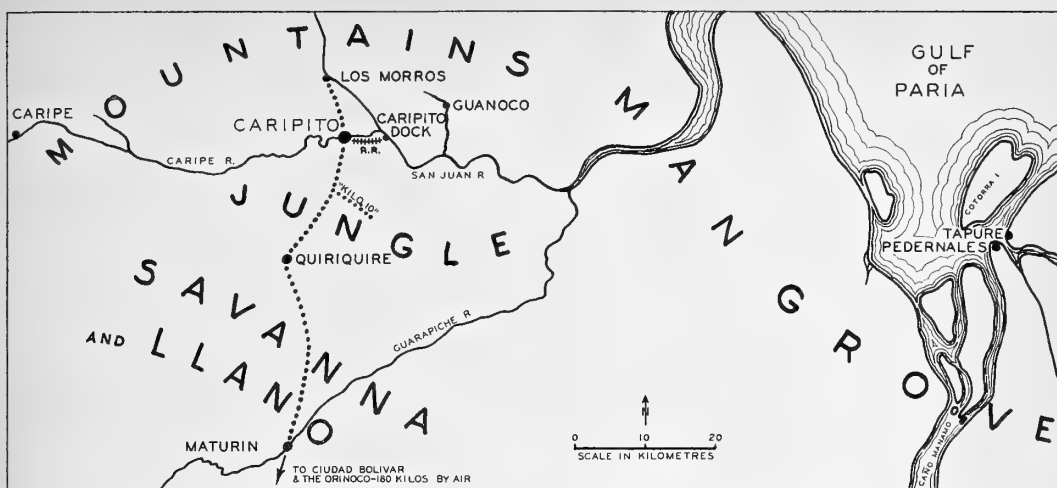
From the southwest and around through north to northeast of Caripito the land rises rather abruptly into hills and mountains. Some of these are close; others, to the west, far away, show horizon silhouettes up to almost 5,000 feet.

The Rio Caripe winds from the west to and through Caripito, and on eastward to its junction with the much larger San Juan. This latter also curves around from the north to the east and on to its ultimate merging with the waters of the Gulf of Paria, looking across to Trinidad and the Paria Peninsula.

From any elevated position in Caripito the horizon seems everywhere bounded by jungle, but this is deceiving, for at its best it is not comparable with the majestic primitive rain forest of British Guiana. The most dominant human mark on all this region is the excellent asphalt, oil and dirt highway which begins at the bank of the San Juan and runs almost due south to Quiriquire and Maturin. This roughly bisects the region in more ways than one.

To the west and south we find the apparently solid jungle becoming lower and lower, giving way at last to the grassy deserts of the savannas and llanos. There has been a good deal of confusion in the use of these two anglicized terms. By llanos we mean flat, grassy lands wholly lacking in





Text-fig. 2. Physical geography of the Caripito region.

trees except along river courses. Savannas have a thin growth, usually widely spaced, of chaparros and other low trees, this type being very evidently intermediate between extremes of regional vegetation.

The llanos, as I have said, are characteristic of immense areas in central Venezuela, and represent a type of country wholly unlike anything in the Kartabo region. The absence of adequately fertile humus and paucity of such necessary elements as calcium, plus the sterile clays and sands make plant life to any great extent an impossibility, except for quick growing grasses, which soon die and last until burned over, or replaced by the succeeding year's meagre crop. The only tree in the savanna near Caripito is the dwarf and agonized chaparro, *Curatella americana*, which thrives or rather exists in this area, and at its best seems more dead than alive. In the llanos proper, another factor working against any appreciable amount of vegetation is the wide-spread inundation during the rains, permitting growth only of water-resistant plants.

To the east of Caripito and of the highway, we encounter the first mangroves, and these increase in extent and purity of culture until, as we proceed down the Rio San Juan, the last palms and other growths die out. Finally, there is left salt or brackish tidal mud in which only mangroves are able to hold their own. This scenery is characteristic of the entire Orinoco delta.

The jungle itself, chiefly to the south and southeast of Caripito, is confusing at first. There seems to be no reason why these *selvas* should not be as tall, as fine, as luxuriant as those of Kartabo, but they simply are not. Occasionally there is a tree so tall, so hung with lianas, that it recalls the finest of the

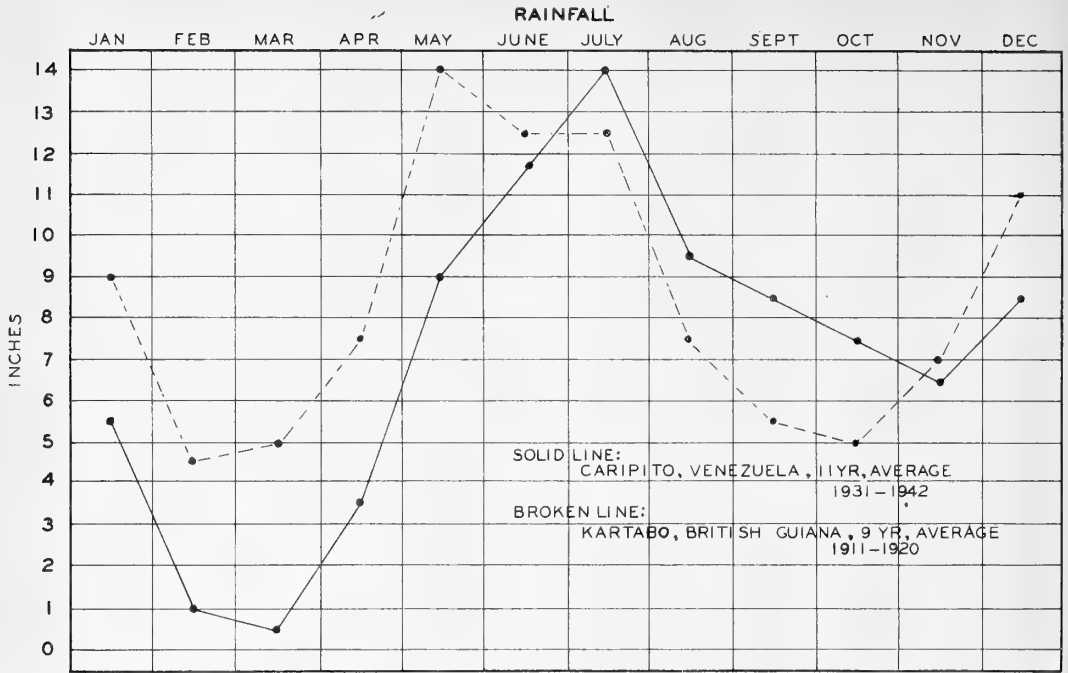
rain forest growth, but on the whole one thinks of it as second growth, as stunted tropical forest. The prolonged and intense drought of the dry season does not seem sufficient to explain this condition. The soil and subsoil are relatively thin but so also is the soil of Guiana. The real answer did not come until a full month or more of the wet season had past, when we found that our so-called jungle had all become first marsh, then swamp, and finally actually inundated. Most of our collecting ground was permanently under water, and this for months.

### SEASONS.

(Text-figs. 3-5; Pl. II, Fig. 2).

The most noticeable thing about the seasons at Caripito is the very long, very pronounced Dry Season. This embraces January, February, March, April and sometimes early May. In these months the rainfall varies from a quarter of an inch (as in March, 1942) to as much as an average of 5.64 in May. Variations occur, as in 1942 when a single downpour of 2.1 inches on the first day of January brought up the month's average to a false rain figure. May of 1942 with 12.35 inches was definitely thrown into the Long Wet Season category.

This second period normally includes June, July, August and September, all usually with 10 to 17 inches of rain. Then comes a slackening during October and November but with no average below 6.73 inches, and rising somewhat in December. This short October-November drop in rain can hardly be considered a second Dry Season, compared with that in the early part of the year or the very definite one which exists in the Kartabo year. Variations in



Text-fig. 3. Comparative rainfall of Caripito and Kartabo.

successive years may shift or completely obliterate this lessened precipitation.

So, in general, we find at Caripito two main seasons: one very dry of four months or slightly more, and the other with a considerable rain average and a sudden high peak in July and another lower one in December.

The difference between the general annual rainfall of Kartabo and Caripito, 100 and 80 inches respectively, would not in itself be sufficient to explain any extreme differences in flora or fauna, but the different distribution into two radically unlike seasons, instead of four less strongly marked ones, may well be considered to be responsible in part for fundamental ecological differences.

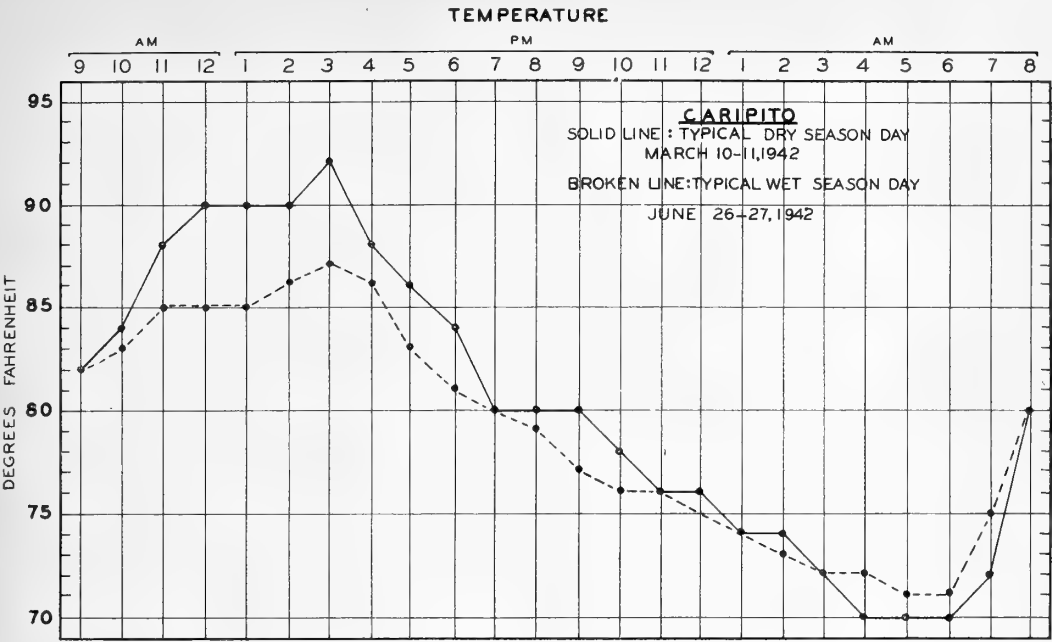
The Caripito data are based on records extending over eleven years, and the general averages are reasonably well balanced. But the extremely local character of the rains and the seasons is shown by comparison with neighboring localities. Caripito rainfall is 80 inches. Quiriquire (27 kilometers south), 60 inches; Ciudad Bolivar (223 kilometers south), 35 inches. Yet these two places are in a direct line south, in the general direction of Kartabo. In each of their rainfalls the January-May dry season is much more pronounced, with low peaks of precipitation in June, July and August.

The number of days upon which rain falls does not differ radically in Kartabo and Caripito. An average Kartabo year shows

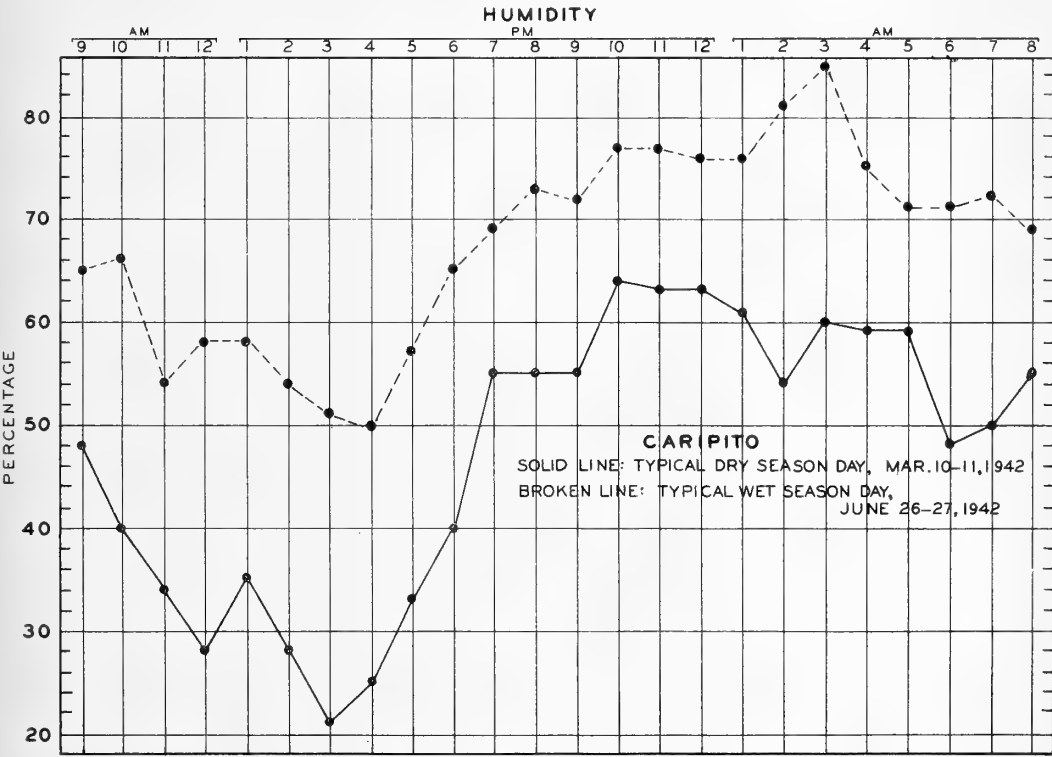
219 days of precipitation, or 59 per cent., and a corresponding Caripito year presents 197 rainy days, which is 54 per cent. of the year. To continue comparison of the same years, that at Kartabo shows May and June with 27 days of rain each, and February with a minimum of 6 days. Caripito has the maximum in May and July with 25 and 27 days respectively, while April has only 5.

Kartabo's maximum and minimum annual rainfalls are 117.75 and 77.11 inches; Caripito's are 104.15 and 61.13 inches. Monthly maximums are, Kartabo 22.34 inches in a May; Caripito 16.90 in July. Monthly minimums are, Kartabo .03 inches in an abnormal February, and Caripito .25 in a March.

The great variability in the character of the immediate environment of Caripito has already been pointed by the fact that less than 20 miles (27 kilometers) away, the annual rainfall is cut 25 per cent. We may develop this at even less distances. For example, the little narrow-gauge railway from Caripito to the loading wharf on the Rio San Juan is only 4.8 kilometers (3 miles) in length, yet at the river terminal there is an increase of 10 per cent. more rain. In returning to Caripito from a day's collecting in full sunshine at Tenth Kilometer on the Quiriquire road, we would often pass definite bands of heavy rainfall, such as three zones of saturated soil and jungle, alternating with two of dusty dryness.



Text-fig. 4. Temperature of typical Dry and Wet Season days.



Text-fig. 5. Humidity of typical Dry and Wet Season days.

A day in mid-March is typical of much of the dry season: early morning and sunset fairly clear, followed by almost immediate overcasting, sometimes by clouds, or more usually, by a dust haze which often is enhanced by thin smoke from distant burning grass. Even with the humidity as low as 22% in the day and 65% at night, the heat seems greater than during the rainy season, although the annual temperature extremes are so very slight, ranging from a December average of 78 to a May average of 84 degrees Fahrenheit.

Everywhere in open country, whether among scattered trees, low bush or grass, everything is parched, dry and dusty. Animal life seems at lowest ebb both in species and individuals. As the dry season progresses, ditches and small streams dry up completely; the Rio Caripe shrinks to a narrow, shallow channel. Many organisms show great suffering. There is a concentration along the banks of the rivers, and elsewhere snakes, lizards, and small mammals become more evident, often coming out into the open in daytime in their search for moisture. The fish, frogs and turtles of the small streams burrow deep into the last damp mud, if they cannot escape overland.

Precipitation of dew seems to keep the superficial, tree-top foliage of the jungle green but an unusual number of trees lose their leaves, although this is more apparent in open areas in isolated cases, than where the deciduity is obscured by the preponderance of evergreen jungle palms and other growths. All low-growing plants and especially those on the floor of the *selvas* reflect the drought of the surrounding country. Climbing plants and terrestrial growths shrivel and die, and every footstep causes a loud clatter of brittle, crackling leaves.

A few rare showers from mid-March on, arouse, now and then, false activities on the part of leaf-buds, insects and the lower vertebrates, but this abortive energizing ends in swift return to patient waiting, or frantic search for the wherewithal to quench an ever-increasing thirst. The actual preshift of the seasons is marked by increased haze and sultriness, greater humidity at night and distant thunder. Even before these symptoms, however, certain plants, like the yellow poui-trees, *Tabebuia serratifolia*, seem to sense the coming change, and burst overnight into solid masses of golden flowers, completely covering the leafless branches.

The actual breaking of the rains (as on April 27 in 1942) produces an effect even more radical and more immediate than the inauguration of the two wet seasons of Kartabo. Every organism from bacterium to the tallest jungle tree, and from protozoan to jaguar and tapir, must be profoundly

affected. Specific details of some of these changes will be considered in papers dealing with separate animal groups.

There is no such thing as a typical wet season day. One of the first effects is the clearing away of all dust haze and smoke, with consequent distinct views of distant mountains. The humidity ranges from around 50 per cent. in the afternoon to 85 or more after midnight, but shifting winds, irregular downpours and rare days of complete clarity and cloudlessness, alternate with every conceivable combination of sun, cloud, rain, humidity and temperature. The latter rarely ascends to 87 degrees Fahrenheit.

As the rains continue, the second climatic extreme becomes evident. From a grateful resuscitation to life, there ensues gradual drenching and flooding, and soon much of the floor of the jungle which was on the way to becoming a parched desert, turns into a shallow, swampy lake, so permanent that hosts of creatures are sent fleeing to low ridges or up tree trunks to keep from drowning.

The low, flat situation of the jungle in general, together with an almost absence of drainage, explains this extreme result of the rains; and helps to account for the general faunal conditions here compared with those of the rain forest at Kartabo.

#### EFFECT OF POPULATION.

Finally, at Caripito, there is the human element to consider. The great oil developments throughout the country have brought about an unusual density of population, not alone in the oil camps but in small villages, old and new. Especially has there been an influx of squatters and resident small farmers. One result is constant hunting and trapping on the part of the natives, to whom hardly anything comes amiss as food. Still more important is the ever-increasing clearing and burning of great portions of the wooded tracts and jungle, especially wherever there is any ground too high to be completely flooded. This has exterminated or thinned out or driven away a noticeable percentage of many forms of animal life, both invertebrate and vertebrate.

The focus of our interest centered in the differences between the fauna of the Kartabo rain forest, which is part of and in the midst of a vast, homogenous, faunal area, and that of the Caripito jungle which is sharply limited and isolated—a bit of low, undernourished rain forest, alternately dried and drenched, insulated by hundreds of miles of open, grassy llanos, abrupt mountains, and the submerged world of mangroves.

## EXPLANATION OF THE PLATES.

### PLATE I.

- Fig. 1. Air view near Caripito, showing merging of jungle and savanna. (*Photograph courtesy of Standard Oil Companies of New Jersey and Venezuela*).

### PLATE II.

- Fig. 2. Bed of the Caripe River at height of dry season.
- Fig. 3. Outlook to north of Caripito laboratory, showing Caripe valley and distant mountains.





FIG. 1.

PHYSICAL FACTORS IN THE ECOLOGY OF CARIPITO, VENEZUELA.







FIG. 2.



FIG. 3.

PHYSICAL FACTORS IN THE ECOLOGY OF CARIPITO, VENEZUELA.



## 10.

On the Locomotor and Feeding Behavior of  
Certain Postlarval Clupeoidea.

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(Plates I &amp; II; Text-figures 1-3).

## INTRODUCTION.

In connection with studies on the life history of the Tarpon being carried on at the laboratory of the New York Aquarium, located on Palmetto Key, Florida, it became necessary to handle and examine all other isospondylous fishes living in that vicinity. Their larval stages were given considerable attention. In connection with this work it was found possible to establish in laboratory aquaria the postlarvae of both *Anchoa mitchilli* (Cuvier and Valenciennes)<sup>1</sup> and *Harengula pensacolae* Goode and Bean.<sup>2</sup> The feeding behavior and locomotor habits of the very delicate juveniles of these species were studied in some detail and found to show certain noteworthy characteristic features. These studies were undertaken by both authors in the summer of 1940 and continued by the senior author during the summers of 1941 and 1942. We are grateful to Dr. Carl L. Hubbs for various critical remarks on some of the items contained herein.

## LOCOMOTOR BEHAVIOR.

The postlarvae of *Anchoa mitchilli* must exert mechanical forces in order to maintain their position at a given depth of water and to maintain their equilibrium. Active and apparently normal postlarvae that had become well established in aquaria were clearly seen to sink when they ceased active swimming. On sickening or on the slightest shock they turned over and sank, ventral side up. Despite their rather large swim bladder,

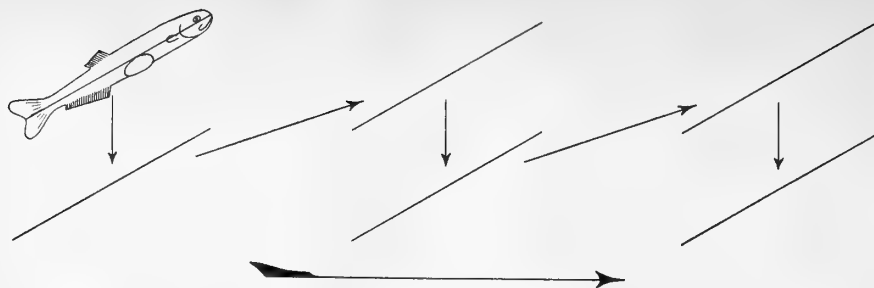
they evidently are slightly heavier than sea water. The position of the swim bladder, below the center of gravity, is obviously an important factor in this unstable equilibrium. Although, as pointed out by Lochhead (1942), the ballistics of a dead or disorganized fish cannot be used for determining their normal hydrostatic or hydrodynamic characteristics, it is at least suggestive.

When not actively feeding, the postlarvae of *A. mitchilli* are usually inclined upward and forward at an angle of about 30° to the horizontal. In this position they sink for about one-half their length and then swim directly forward, thus regaining their former position in regard to depth of water and coming to rest in advance of their original location at a distance about equal to one and a half times their own length. They then sink and repeat the locomotor performance again and again. This gives them a forward translation interrupted by sinking movements about as indicated in Text-figure 1. These postlarvae exhibit strong schooling tendencies and this mode of progression is most frequently seen in a broad, quietly milling school.

The specific gravity of the adult anchovies seems to be closer to that of the sea water, but they are evidently still a little heavier than the surrounding medium, for they show a bare suggestion of similar correction, by swimming efforts, of a tendency to sink. Superficially the tendency to turn over is not evident in sound specimens, either adult or postlarvae, but the pectoral fins are seen to be in constant irregular motion, as though beating down to correct an ever-slight roll, that cannot be otherwise detected. The adults, like the postlarvae, sink back-down when about to expire. Fin-clipping or other methods of direct approach are not

<sup>1</sup> According to Hildebrand (1943) all the material found in the vicinity of this station is referable to the race *A. m. diaphana* Hildebrand. He discusses the situation in considerable detail.

<sup>2</sup> According to Storey (1938) this name, rather than *H. macrophthalmus* (Ranzani) as used by Breder (1942 b), is applicable to the form found in this locality.

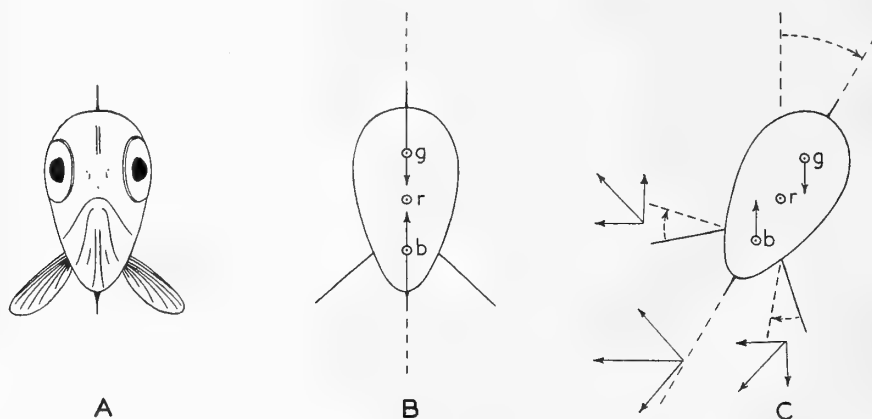


TEXT-FIG. 1. Swimming movements of larval anchovy, indicating extent of sinking and extent of forward and upward swimming. The fish figure is represented at the end of each successive sinking and swimming period of an axial line, the arrows indicating the direction of translation.

practicable in these exceedingly fragile fishes, for even the most gentle handling produces the disturbances described above. Conversely, when large numbers are handled, a few individuals do survive tow-net operations and can be established in aquaria.

As nearly as can be interpreted from simple observation, the anti-roll mechanism works about as follows. The apparent activity of the pectoral fins is indicated in Text-figure 2 in which "A" shows a front view of a mature anchovy with the pectorals in the position they take as they beat irregularly on each side. Careful and repeated checking indicates that what actually takes place is something like that shown in the rest of Text-figure 2. In "B" is shown a body like that of *Anchoa* with "g," the center of gravity, higher than "b," the center of buoyancy, respectively above and below "r," the center of roll. The pectoral fins, when thrust out as indicated in "A," form, even when they are at rest, an impediment to the rolling couple inherent in the posi-

tions of "g" and "b." When rolling once starts as indicated in "C" it is corrected by quick movements of the right and left pectorals in opposite directions, as indicated. That is, in a roll to the right, the right fin beats down and the left up. The fins are then immediately folded close to the body and then thrust out in the position shown in "B." It will be noted that position "B" makes them equally available for checking a roll to either side. It is these movements of the fins that can be detected and are what have been previously referred to as irregular. It must be borne in mind, however, that these movements are very slight and rapid and not easy to see. They are exaggerated in the diagrams shown in Text-figure 2. Vector diagrams in "C" indicate the components of each pectoral and their resultant as well as their combined values as a reaction force against the vertical center of the fish. For further analyses of such vectors see Breder (1926) and Breder and Edgerton (1942) and for other considera-



TEXT-FIG. 2. Equilibrium maintenance in *Anchoa mitchilli*. **A.** Front view of fish, showing disposition of pectoral fins at rest; diagrammatic. **B.** Front view of a body such as an anchovy in unstable equilibrium. g—center of gravity. b—center of buoyancy. r—center of roll. **C.** Dynamic checking of an incipient roll by action of the pectoral fins. Lettering as in "B." See text for full explanation.

tions on the role of the paired fins in reference to equilibrium see Harris (1936, 1937, 1938).

Between these correcting movements there is an intermittent simultaneous down beating of the pectorals which lifts the head for swimming upward and forward, as indicated in Text-figure 1. It may also be that these fish are slightly head-heavy as in the downward sinking of a weakened or dead specimen the head tends to lead the tail, but this may be due to the streamlined form and its consequent tendency to orientation.

The swimming of these fishes agrees well with the method of sinking and swimming by jerks as discussed by Lochhead (1942) who gives an excellent discussion of the hydrodynamics involved. Normally these fish do a considerable amount of chasing about in the open sea but on very wide flats of shallow water the schools often attain a fairly quiescent state in the vicinity of pilings. Similar reactions are seen in aquaria and are presumably associated with a restricted volume of water. Incidentally one of the specimens had a copepod attached to its dorsum. This fish, which may be seen vaguely in Plate II, Fig. 6, had completely compensated for this added material and could not be separated from its fellows on a basis of behavior. It must be borne in mind that the above-discussed corrections of tendencies to sink as well as that to roll over are maintained in the face of several continually varying factors. For example, every bit of food ingested, the progress of digestion and the voiding of excrement alters the delicate balance between the values of "g" and "b" and shifts their position fore and aft. Such observations have a direct bearing on the work of Lochhead (1942) in that they refer his concepts to an immediate minute to minute basis.

In *Tarpon atlanticus* respiratory gulps influence buoyancy, as may be seen from their tendency to sink and the associated fin movements of the pectorals, which are not unlike those described for the very much smaller anchovy. Observations in an aquarium of tarpon ranging from about 6 to 100 cm. indicate that they seem to become heavier as the time for them to rise for breath approaches. Their pectorals typically work harder and finally with a burst of tail effort they rush to the surface and gulp. It may be that in clear, well-oxygenated water this is what actually triggers off the impulse to rise and gulp. After the ingestion of air they are usually lighter than water and frequently have difficulty descending until they emit small bubbles by way of the gill clefts, after which they reach a state of approximate balance and from then on become heavier again. It would seem that this increase in specific gravity is associated with the fact that their gills are also functional

and that there would seem to be a progressive loss of buoyancy by the branchial elimination of  $\text{CO}_2$ . For further details on the respiratory rises in the Tarpon see Shlaifer and Breder (1940), Shlaifer (1941) and Breder (1942 a).

The comments made above apply to *Harengula pensacolatae* quite as well as to *Anchoa mitchilli*. The physical differences and similarities of the two species is evident in Plate II. Even after it has reached the adult form, *Harengula* clearly shows the intermittent sinking as diagrammed in Text-figure 1. A photograph of a small school of these fish of about 30 mm. in standard length is given in Plate I. The angles of five fish, that are clearly side on, are  $22^\circ$ ,  $33.5^\circ$ ,  $32.5^\circ$ ,  $32.5^\circ$  and  $40^\circ$ , with a mean of  $32.1^\circ$ , in reference to the horizontal as indicated by the frame of the aquarium in the background. This mean angle is very close to the estimate of  $30^\circ$  for the postlarvae of *Anchoa*. The photograph was taken just as most of the fish had reached the bottom of their sinking movement. It will be noted that they not only all head nearly in the same direction but that they are mostly in closely similar stages in regard to the sinking-swimming movements. A young *Mugil cephalus*, otherwise alone, had attempted to school with the herrings and is seen in front of one of them. This species does not take on the sinking-swimming type of movement, at this size at least, and its attempts to school with the herrings were eventually given up. The school formation was disrupted by darkness, for its basis is clearly visual, as in most fishes (Newman, 1876; Parr, 1927; Breder, 1929; Spooner, 1931; Bowen, 1931, 1932; Breder and Nigrelli, 1935; and Shlaifer, 1942).

#### FEEDING BEHAVIOR.

The approach of the postlarval anchovies and their manner of address to an intended food item is most striking, and is more marked in the smaller and more leptocephalus-like individuals. They do not simply swim up to a planktonic bit of food and engulf it as might be expected. In these reactions they contrast with most fishes of similar size and state of development that are more customarily kept under conditions permitting close observation of feeding habits. Postlarval anchovies about 15 to 20 mm. long, as seen swimming, appear to be rather stiff-bodied little creatures. Instead of merely darting at the food object, they follow it for a time in a typical stalking approach. Finally they orient themselves in such a position as to "point" it, at which time they draw themselves into a more or less S-shaped form with the head pointing straight at the object. As soon as this "stance" is established the fish straightens



TEXT-FIG. 3. The feeding strike of *Anchoa mitchilli*. **A.** Lateral view of successive positions of the poise for striking and the follow through. **B.** Dorsal view of the same positions. See text for full explanation.

itself out with extreme rapidity, springs forward by the impetus and ingulfs the food. There is a "follow through" of a long sweeping curve that terminates in the normal stiff-bodied swimming attitude. The sequence of these attitudes as seen from the side and from above is shown in Text-figure 3. Plate II shows a variety of poses of these fish, Figure 6 showing the extreme of the S-shaped flexure. The approach to the food item was always made from at least slightly below. In this connection it should be mentioned that in tow-net drags made in the daytime these fish were always found to be much more abundant in samples taken near the bottom rather than in surface tows. Only on dark nights could they be taken in any quantity at the surface. It may be that these fish are accustomed to look up while feeding, silhouetting the plankton against the surface light. The fact that these fish rose to the surface in the sea on dark nights might be associated with a negative phototaxis, daylight merely holding them down. A bright light above an aquarium would force them to a lower level.

As the fish increase in size and gradually transform into juveniles they give up this behavior and substitute for it the usual fish habit of darting at food. Frequently, however, they lapse into a more or less typical postlarval behavior pattern.

The relatively shorter and deeper bodied postlarvae of *Harengula* perform in as similar a manner as their physical attributes permit. Such a fish in its less emphasized "S" striking stance is shown in Plate II, Fig. 8. By the time they have reached the size shown in Plate I such behavior is given up and would likely be impossible because of the increasing stiffness and thickness of the body.

The juvenile pattern of food taking, as here described, certainly seems unnecessary. The food objects, plankton of various kinds, move so slowly as compared with the activities of the much larger fry, that a "pounce" of any kind seems ridiculous. In fact it might be likened to a small boy getting into a certain "striking" position to pick up a slowly walking box turtle. Furthermore these plankton organisms were never

seen to make any avoiding reactions to a fish passing near, and if such were made they would surely be ineffectual. Most of the food organisms taken were crustaceans, of the many kinds in which the local waters abound. The fish were noted at times to approach but pass by planktonic forms of relatively moderate size, but which were still too small to make successful avoiding reactions. This behavior was noted as the postlarvae fed, thrived and grew, on such plankton material as was brought to them, mostly by replenishing the sea water in the standing aquaria. Some of these fishes were successfully shipped to the old New York Aquarium and here the same reactions were observed to be successful on newly hatched *Artemia*, a form which they never encountered in the sea, strengthening the view that this behavior is in no way an accommodation to any particular type of organism.

### DISCUSSION.

The mechanical features of maintenance of equilibrium by these postlarval fishes is sufficiently evident, but the reasons for the reactions involved are not clear. The relative merits of solid stability and a delicate instability, as discussed by Lochhead (1942), would seem to be the only current view that could be expected to lead to a thorough understanding of this situation. The sinking-swimming movements would seem to be of an adequate magnitude to easily permit of a proprioceptive control of the kind he visualizes. At least these fishes hold their level in an aquarium at night, as was repeatedly demonstrated by flashing a light.

It is difficult to imagine that the peculiar feeding behavior has any particular value in the open sea to fishes that are so much faster than the relatively inert planktonic forms on which they feed. If, on the other hand, one considers the history and relationships of these fishes certain suggestions appear. Since many of the Isospondyli and Apodes agree in having leptocephalus or leptocephaloid postlarvae, the resemblances in the postlarval forms suggest a community of origin, which, as Gregory (1933) indicates, helps reinforce various osteological evidence. He writes, "... the 'leptocephalus' larvae of the eels is very similar to that of the isospondyle *Albula*, while the skull of eels seems to be merely a highly specialized derivative of some large-mouthed Cretaceous isospondyle type. *Thrissopater* (A. S. Woodward, 1909) might be such a form, except that the supraoccipital is in contact with the frontals, while in the eels it is separated from them by the parietals. The recent *Engraulis* among the clupeoids shows that the hyomandibular may easily become secondarily directed backward."

In connection with the present discussion

an examination of the feeding behavior of the postlarvae of apodal fishes should be of interest. Apparently no such study has been made. Dean (1912) described the swimming behavior on the part of an eel leptocephalus, but unfortunately nothing of its feeding habits. Actually the striking of larval anchovies reminds one strongly of the striking of an adult moray. This in itself may be entirely mechanical; the sea snakes also strike in this fashion. This is in fact, about the only way in which an eel or caudally compressed snake-like form can make a sudden dart when floating freely. In the case of the postlarvae under discussion, however, it should be emphasized that they are not to be thought of as eel or snake-like in length; they are much too short-bodied to derive any special benefit from this eel-like behavior. Actually a more typical fish strike would seem to be just as serviceable to them.

Instability of equilibrium is widespread in the Isospondyli, as is indicated by the reference to adult tarpon, and is apparently a very old feature. For this reason it does not seem likely that this feature of the Isospondyli can be of much significance in such a consideration of the bearing of phylogeny on habits.

It may be that there is some connection between this type of instability and the feeding habits described, an item suggested by Dr. Hubbs. If this is the case, for the reasons already outlined, the mechanical connection between the two features is certainly not evident from any of the data as yet at hand. Very likely both items are widespread among the Isospondyles. Hubbs (1941) points out that a variety of unrelated fishes have independently developed postlarvae which are similarly sub-leptocephaloid in appearance. It would be of interest to compare the feeding behavior and stability characteristics of the postlarval Isospondyles, Apodes and those scattered through other groups. Until something of this nature is undertaken little can be done to separate the items of physical necessity from those of heritage.

### SUMMARY.

1. Postlarval *Anchoa mitchilli* and *Harengula pensacolatae* are in unstable equilibrium because the center of gravity is higher than the center of buoyancy, while the fishes as a whole are slightly heavier than the water they inhabit.
2. Equilibrium is maintained by mechanical efforts of chiefly the pectoral fins and locomotion proceeds by an alternating series of sinking and swimming periods.
3. These features largely but not com-

pletely disappear as the adult form is reached.

4. These postlarvae feed on small plankton organisms which they stalk and strike in an eel or snake-like manner, a procedure apparently quite unnecessary to catch the relatively inert planktonic particles.
5. This feature of feeding disappears as the adult form is reached.
6. The instability of Isospondyles is widespread and the behavior of the young in this regard is too generalized to be useful at present in understanding relationships.

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## EXPLANATION OF THE PLATES

## PLATE I.

Fig. 1. A group of *Harengula pensacolae* in a typical schooling formation. Most of the fish have just about reached the bottom of a sinking movement and show the typical angle at which they hold themselves. A *Mugil cephalus* which has temporarily joined the school is to be seen just left of center in front of one of the herrings.

## PLATE II.

Fig. 2. Dorsal view of a larval *Anchoa mitchilli* against a light background. Actually the fish under such conditions is even less visible than appears in the photograph. Usually about all that can be seen under such conditions are the black eyes. Here the centrally located swim bladder can be discerned.

Fig. 3. A pose similar to that of Figure 2 but with the fish showing about the greatest flexure of the body to be seen under ordinary swimming activity.

Fig. 4. A lateral view of *Anchoa mitchilli* indicating a typical pose with reference

to the horizontal. The light spot behind the eye is caused by an argenteous layer catching the light and showing through the transparent skin.

Fig. 5. A ventral view of *Anchoa mitchilli*. The interruption of the dark line indicates the position of the ventral fins.

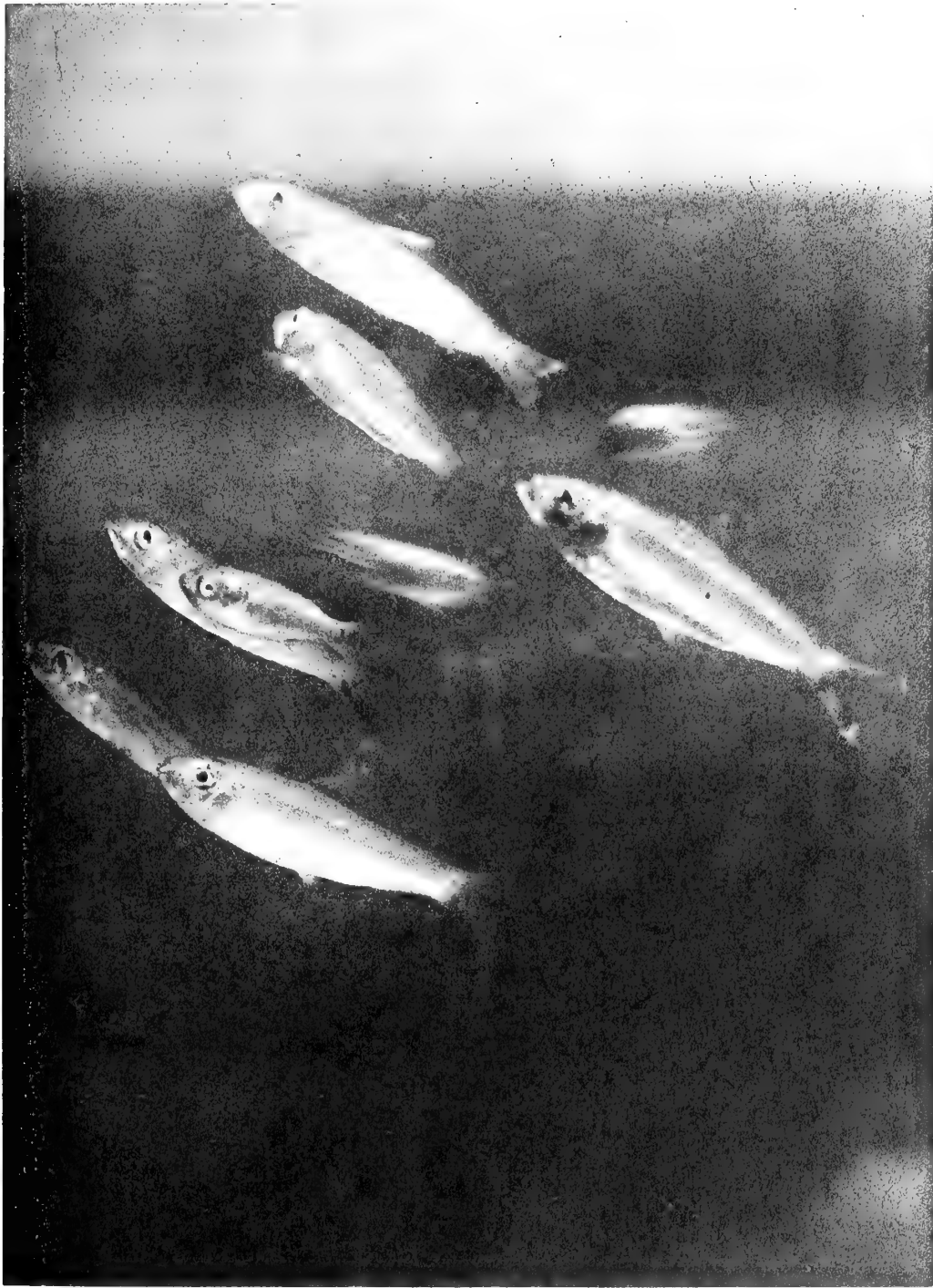
Fig. 6. The typical striking pose at about its greatest point of flexure, just before the fish straightens out and lunges forward. The fish in the background has a parasitic copepod attached near its dorsal fin.

Fig. 7. Another view of *Anchoa mitchilli* striking. Here the fish is partly straightened out as it lunges forward.

Fig. 8. *Harengula pensacolae* partly arched for striking. This fish is of a size nearly ready to abandon the habit. The rather large particle at which it is preparing to strike may be seen not quite a head's length beyond its snout.

Fig. 9. *Anchoa mitchilli* photographed against some verticals and including the water level surface of the aquarium. This represents the steepest angle from the horizontal that these fishes ordinarily reach.





ON THE LOCOMOTOR AND FEEDING BEHAVIOR OF CERTAIN POSTLARVAL CLUPEOIDEA.





FIG. 2.

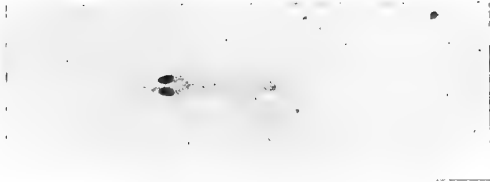


FIG. 3.



FIG. 4.



FIG. 5.



FIG. 6.



FIG. 7.

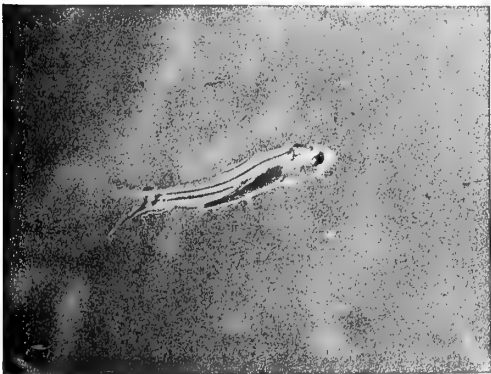


FIG. 8.



FIG. 9.

ON THE LOCOMOTOR AND FEEDING BEHAVIOR OF CERTAIN POSTLARVAL CLUPEOIDEA.



## 11.

## A Revision of the Subfamily Estrildinae of the Family Ploceidae.

JEAN DELACOUR.

(Text-figure 1).

The thick-billed passerine birds generally known as finches have always aroused much human interest. They belong to a large number of species, the majority of which eat mostly seeds, are adapted to life in open country and have consequently taken well to the artificial conditions created by mankind, benefiting from agricultural cultivation. They have increased in number while less adaptable forest dwellers have decreased, and they are at present familiar inhabitants of our gardens, orchards and fields the world over. Most of them sing well; many are of attractive shape and colors; they are easy to feed, generally speaking, as they usually thrive on a diet of readily obtainable seeds, accordingly becoming popular cage birds. It is, therefore, only natural that they have attracted widespread attention.

But if their life habits have long been comparatively well known in the wild state and in captivity, finches have been less fortunate with systematic ornithologists. Until recently, they have been very arbitrarily classified according to relatively unimportant morphological characters. Only during the last thirty years was great progress made in the understanding of their true affinities. It now appears that the so-called finches consist of several distinct and not closely related groups of birds, whose thick bills, an adaptation to a seed diet, have been acquired independently in different families. But a further discussion of this important question is outside the scope of the present paper.

The whole finch group has been particularly well studied by the late Peter Sushkin (*Bull. Br. Orn. Club*, vol. XLV, pp. 36-39, London, Dec. 5, 1924) who discovered and interpreted valuable anatomical features; but several years earlier, James Chapin had already published "The Classification of the Weaver Birds" (*Bull. Amer. Mus. N. H.*, vol. XXXVII, Art. IX, pp. 243-280, New York, May 8, 1917) an exceedingly valuable contribution to the position of an important division of the thick-billed birds, the Ploceidae family. It was followed by another paper by Sushkin on the anatomy and

classification of the weaver birds (*Bull. Am. Mus. N. H.*, vol. LVII, Art. 1, pp. 1-32, New York, Oct. 24, 1927).

The three contributions just mentioned marked the start of a new era in the study of these birds. Since that time their authors' conclusions have been adopted and developed by all serious ornithologists.

About ten years ago, I published a "Monographie des Veuves" (*L'Oiseau*, Paris, 1933, pp. 521-562, 667-726; 1934, pp. 52-110), a detailed revision of two groups of weavers which had long been more or less confused, embracing the various species composing the two large genera *Euplectes*, of the Ploceinae, and *Vidua*, often associated with the Estrildinae, but which I consider to form a special, intermediate and more primitive subfamily, the Viduinae. In the above work, I was helped by M. F. Edmond-Blanc, who had a great deal of experience with weavers in their native countries and in aviaries; I am personally responsible for the systematic arrangement.

At that time, ten years ago, I had already promised myself to undertake a revision of the numerous, diversified and highly specialized members of the subfamily Estrildinae, popularly known as waxbills, grassfinches and mannikins, a most interesting gathering of beautiful little weavers, the largest of which is rather smaller than an English sparrow, while most of them are small, some even very small, certain kinglets, sunbirds, hummingbirds and a few others only being of equal or still inferior size.

Only this year was I able to study them thoroughly, thanks to the remarkable preparatory work done by my friends Drs. J. Chapin and E. Mayr in rearranging the large and excellent collections of these birds in the American Museum of Natural History. The present work has been based on them, and no better or larger series exist now in the whole world.

The old system of separating the Ploceidae into two subfamilies according to the size of the first primary, longer or shorter than the primary covert, and to that alone, is so obviously unnatural and wrong that it

was doubted as long ago as 1850 by Bonaparte, and afterward by Newton and even by Shelley, who, however, somewhat reversed his opinion later on.

Aviculturists who have kept, bred and studied weavers in captivity for well over a century, always more or less openly refused to adopt this artificial classification. This is quite evident in the avicultural literature. The late Dr. A. G. Butler, in particular, worked a great deal with these birds and published many articles and several volumes on them and their allies. His principal work, "Foreign Finches in Captivity," London, 1899, is an excellent book, full of the most useful biological information and systematic suggestions. The classification that he proposes, only from the amateur's point of view, as he puts it very unpretentiously, is for a great part perfectly acceptable, if still too respectful of old prejudices. Dr. Butler wrote as an aviculturist, but he was at the same time a professional entomologist at the British Museum, and an accomplished all-around naturalist.

In order to come to a better understanding of the position and affinities of the numerous forms of the subfamily Estrildinae, the first step to be taken is to formulate their principal characteristics. The deepest, most ancient and significant features must be considered first. Apart from the primordial anatomical particularities pointed out by Sushkin (*loc. cit.*), the really important characters in these birds seem to be as follows:

1. *Mouth marking in nestlings.* All very young Estrildinae show brightly colored, swollen bands or spots at the gape, and dark spots or lines on the palate or the tongue, or on both. Viduinae, an allied subfamily whose members are all parasitic on Estrildinae, show the same features, probably a late adaptation caused by parasitism.
2. *Color pattern of plumage.* Very highly specialized and diversified in Estrildinae, much more so than in any of the other weavers. Immatures always have a special dress, different from that of the adults of both sexes, which are unlike in a number of species, but often only to a slight degree. Females, when different from the male, always possess an elaborate plumage. The striated, sparrow-like brown livery which is worn by all immatures, females and males in eclipse, of the Ploceinae and Viduinae, is never found among Estrildinae, in either sex. With the one exception of the Indo-Malayan *Estrilda amandava*, no member of the Estrildinae has a seasonal eclipse plum-

age; even in this unique case, it bears no relation to the primitive eclipse dress of the Ploceinae and Viduinae.

3. *Life habits.* Estrildinae never weave elaborate nests like the Ploceinae. They build large, rough balls of grass and leaves, with a side entrance, which are usually located near or on the ground, in tough grass or bushes. They are not parasitic nor do they scratch the ground in search of food, like the Viduinae. They lay a large number of eggs, always white. Their courtship and voice vary in the different groups and constitute excellent discriminating characters second only to mouth markings in juveniles.

The above three groups of characteristics are the only ones that are truly diagnostic as far as subfamily and tribe go. Morphological characters, long considered of first importance, are really secondary and can only be used for lower divisions, generic, subgeneric and specific:

- a. *The bill* in Estrildinae varies greatly in shape, length, thickness and color. As in all Ploceidae, the culmen is more or less extended back in a wedge between the feathers of the forehead. It is usually brightly colored, never horny brown, a primitive feature. Its shape is of value and often distinctive of genera and subgenera, but its size varies very much according to species and subspecies. Over-estimation or faulty interpretation of its significance has led to many mistakes.
- b. *The legs* do not vary much in the whole sub-family, but the toes become increasingly long in the mannikin group, where they provide good subgeneric or specific characters.
- c. *The tail* may be long or short, narrow or wide, rounded or graduated, or even sharply pointed, but it varies very greatly in length in obviously closely related forms and, on many occasions, it is of no more than specific value. The upper tail-coverts, in several species, are lengthened, decomposed and brightly colored.
- d. *The wing formula* was previously considered of paramount importance but this view has been abandoned since its relative insignificance has been pointed out by Chapin and recognized by Sushkin and others.

The old, but largely wrong, classification of finches and weavers rested on the absence, presence and size of the first or outermost of the ten primaries. In fact, this feather is always present. It is almost invisible (very small and rotated to a concealed position on the dorsal side of the



wing) in many groups: Fringillidae, Emberizidae, Passerinae; it remains very short and pointed in several Ploceinae (*Euplectes*), the Viduinae, and in all Estrildinae except *Clytospiza* and *Spermophaga* where it is well developed. It is larger, but in various degrees in most Ploceinae. A large first primary is in fact no more than a primitive character, which shows up in various groups and does not indicate any close connection between them. It is only of generic value. As Sushkin has said, a declining organ cannot serve as a taxonomic criterion.

The relative length of the other primaries also is only of minor importance. In several cases it is useful as a subgeneric character, while in others it is only a specific feature, as changes are irregular or gradual among closely allied forms. This happens in the large genus *Estrilda* where they seldom accompany other more important differences, and they never can constitute a generic distinction. The shape of the second primary is also variable and of no great importance. In the majority of species, it is normal in its general shape, broader or narrower and more or less pointed. But in all *Pytilia* and in a number of *Estrilda* of the subgenus *Lagonosticta* (*senegala rubricata*, *larvata*) it is compressed near the tip, pointed and cut away, showing a distinct notch. This is hardly visible and somewhat individually variable in *Estrilda* (L.) *rara* and in *E. angolensis*; it is absent in all other species, including *Estrilda* (L.) *rufopicta*, *caerulescens* and *jamesoni* which in all other respects are extremely similar to the species with a notched second primary. It cannot therefore be of but specific significance.

Taking into consideration all the above enumerated characteristics in the light of their real importance, I have come to the following conclusions:

The subfamily Estrildinae can be divided into three large natural groups, which I shall call tribes: Estrildae (waxbills), Erythrurae (grassfinches), and Amadinae (mannikins). Each of them contains respectively: the Estrildae, 9 genera (*Parmoptila*, *Nigrita*, *Pytilia*, *Hypargos*, *Cryptospiza*, *Pirenestes*, *Spermophaga*, *Clytospiza*, *Estrilda*); the Erythrurae, 3 genera (*Zonaegeinus*, *Poephila*, *Erythrura*), and the Amadinae, 3 genera (*Padda*, *Amadina* and *Lonchura*), some of which in turn can be split into several subgenera. These divisions seem necessary to give an adequate idea of the relationship of the birds to one another. It must of course be understood that in current nomenclature, only the generic, specific and subspecific designations can be included in the scientific name.

Several of the different genera tentatively

included by Chapin, Selater and others in the Estrildinae do not seem really to belong to this subfamily.

I have removed the genus *Vidua* (subgenera *Hypochoera*, *Vidua* and *Steganura*) for which I have created a special subfamily (see reasons in "Monographie des Veuves," *L'Oiseau*, 1934, p. 523.)

I am also unable to include in this subfamily the genera *Pholidornis* and *Anomalospiza*. The streaked plumage of *Pholidornis*, the anatomy of its tongue, and the shape of its bill, as well as the proportions of its wings and tail, appear to remove it considerably from the Estrildinae. Its suggested similarity to *Parmoptila* seems entirely superficial. I could reverse my opinion only if it was found that the nestling shows beyond doubt the mouth markings peculiar to the waxbills. Until then, I shall agree with Bates who placed these birds near *Hylia* in a separate family (Hyllidae) between the zosterops and the sunbirds. (Handbook of the Birds of West Africa, 1930, p. 462).

*Anomalospiza imberbis* is nothing but a Ploceine weaver. Like many of them, the male has a distinct breeding plumage, yellow below, olive streaked with dark brown above. The "sparrow-like" streaked brown plumage of the males in eclipse, females, and immatures is similar to that of many of the Ploceinae. Its short first primary is like that of *Euplectes*. *Anomalospiza* has a very peculiar bill, somewhat recalling in shape that of *Pirenestes*, but of the same colors as that of the average Ploceinae, changing according to season. Another peculiarity of this bird is its parasitism, which has now been ascertained. Van Someren found its young in the nest of a *Cisticola*, and Austin Roberts found its young in a nest of *Prinia flavicans*. In this peculiar habit, *Anomalospiza* recalls the Viduinae, which also are all parasitic, but this fact does not seem to imply near relationship. Each species of *Vidua* is the parasite of one or several closely related forms of waxbills, and the specificity of this adaptation is proved by the almost identical mouth pattern of the nestlings and juvenile dress of the parasite and of its victim.

*Anomalospiza* appears to be a more or less indiscriminate parasite on various small warblers, a less advanced stage in parasitism than that of the Viduinae. So far we do not know that the nestling of *Anomalospiza* has any Viduine and Estrildine mouth pattern, and it is better placed at the end of the Ploceine weavers, in the vicinity of *Euplectes*.

In the light of the above remarks, the subfamily Estrildinae can be defined as follows:

Small weaver-finches of highly specialized color pattern, never showing a primitive

streaked sparrow-like brown plumage and horn-colored bill; sexes alike or different; immatures always different from adult females. No eclipse plumage in males, with one exception. Nestlings always showing brightly colored, swollen spots, lobes or bands at the gape, and an ornamentation of the tongue or palate, consisting of spots or lines. Eggs numerous and always white; nests globular with a side entrance, but not woven. Young birds become adult within a year of their birth and are then able to breed, while it takes two years for young Viduinae and Ploceinae to mature. Peculiar song and courtship variable but consistent, in a general way, in large groups of genera. Ten primaries in the wing, the first being very short and falcate, with the exception of two genera (*Clytospiza* and *Spermophaga*) where it is moderately long. Not parasitic.

As pointed out above, there are obviously three major divisions, or tribes, in the subfamily: the waxbills, the grassfinches and the mannikins.

- A. The first one, the waxbills (Estrildae) is composed of birds whose nestlings show brightly colored warts or lobes at the gape and dark spots regularly arranged on the palate or the tongue. These spots on the palate vary in shape, in size, and in number from 7 (*Poephila phaeton*) to 1 (*Pytilia melba*), even disappearing in the exceptional case of two species (*melanotis*, *phoenicoptera*). In most cases there are black marks on the tongue. All waxbills have high-pitched, chirping or sweet calls and song, much like the true Cardueline finches, and they utter their beak upward. Often, the courtship of the male includes a dance during which he holds in his beak a blade of grass, which he seems to offer to the female and drops at the right moment. In addition to these two main characteristics, waxbills differ from the two following groups in their general shape and proportions; their head is comparatively smaller, their legs longer and their toes shorter; their wings and tails are proportionately longer; they are more elegant, more active and more spritely. The majority of waxbills are Ethiopian and they are represented by only two species in Asia and Malaysia and one in Australia (*Estrilda formosa*, *E. amandava*, *E. temporalis*).
- B. The second group, the grassfinches (Erythrurae), is intermediate between the other two. The mouth markings of the nestlings are nearer to the waxbills, but they have an unmelodious voice, clucking, mournful, trumpeting, metallic or low, never sweet, chirping and finch-like. Their song and courtship are very peculiar, different from those of the waxbills, and more similar to the mannikins'. The cock sits still, the flank feathers puffed out, the neck extended vertically and the beak turned downward, while he emits, apparently by a great effort, a kind of melody, sometimes inaudible. At the same time, he raises himself up and down with a lateral twisting. There are many degrees and minor variations in this ventriloquial performance according to species, and those of the genus *Zonaeginthus* include grass offering. The grassfinches are less quick and are heavier than the waxbills, but less clumsy than the mannikins. Some are nearer in looks to the waxbills (*Zonaeginthus*, *Poephila phaeton*, *P. ruficauda*), while others recall more the mannikin (*Poephila modesta*). These similarities, however, are only superficial and the whole group clearly stands between the other two. The link that the grassfinches provide constitute the very reason why the waxbills and the mannikins cannot be separated in two different subfamilies, as Sushkin and myself had tentatively suggested previously. All grassfinches have highly elaborate plumage and some of the most beautiful birds are found among them. Their bills are usually of a vivid color. Sexes are either alike or different, in almost equal proportion. They inhabit Australasia and Malaysia, one species (*Erythrura prasina*) extending its range to S. E. Asia (N. Laos). Australia is their stronghold.
- C. The third group, the mannikins (Amadinae) is characterized by a special pattern of the mouth of the nestlings. Their palate shows horseshoe-like dark lines or large blotches. The gape has a more or less swollen line, but no warts or lobes. The voice differs according to species, but in general it is like that of the grassfinches, clucking or trumpeting, and their song dance is the same sort of a ventriloquial performance, even more static. Mannikins are heavier still; their bill and head are massive, the wings and tail short, their body long. The toes and nails are very long and slender in several species. Their general appearance is clumsy. They are garbed in more somber hues than the waxbills and the grassfinches, but their plumage remains highly specialized; various vivid shades of reddish and yellowish-brown, black, gray and white, disposed in showy patterns, constitute elaborate dresses. Their bill is either silver or lead gray, or black, one species having it pink (*Padda oryzivora*), another one black and red (*Lonchura nana*) and two others (*Amadina*) flesh color or gray.

With the exception of the genus *Amadina*, where differences are slight (absence or presence of red on the head or throat), both sexes are alike or nearly so, in all species of mannikins, and immatures have a plainer dress, very similar to that of many waxbills. Mannikins inhabit the whole distributional area of the sub-family and are particularly numerous in the Malaysian and New Guinean regions.

As long as the mouth pattern of every species has not been finally recorded, some doubt will remain as to the position of a few species. But judging from our present knowledge which extends to members of most genera, the chance of mistakes is slight. It is, however, very necessary that everyone who has an opportunity to examine nestlings of Estrildinae, in the field as in aviaries, never neglects to register this most important characteristic.

The mouth pattern of the following species has so far been accurately recorded: *Spermophaga poliogenys*, *S. guttata*, *Clytospiza monteiri*, *Pirenestes ostrinus*, *Hypargos nitidulus*, *Nigrita canicapilla*, *N. luteifrons*, *N. fusconata*, *Parmophila woodhousei* (*jamesoni*), *Pytilia melba*, *P. phoenicoptera*, *Estrilda rara*, *E. senegala*, *E. rubricata*, *E. angolensis*, *E. granatina*, *E. ianthinogaster*, *E. erythronotos*, *E. astrild*, *E. melpoda*, *E. nommula*, *E. atricapilla*, *E. melanotis*, *E. capistrata*, *E. subflava*, *E. amandava*, *Zonaeginthus pictus*, *Z. guttatus*, *Poephila phaeton*, *P. guttata* (*castanotis*), *P. bichenovi*, *P. cincta*, *P. acuticauda*, *P. personata*, *P. gouldiae*, *Erythrura psittacea*, *Padda oryzivora*, *Amadina fasciata*, *Lonchura fringilloides*, *L. malabarica*, *L. bicolor*, *L. cucullata*, *L. pectoralis*, *L. striata*, *L. punctulata*, *L. castaneothorax*.

The nearest relations of the Estrildinae would seem to be the Viduinae, their specific parasites. The Estrildinae, however, are a good deal more specialized than the Viduinae and represent the most advanced branch of the whole family Ploceidae. As there exists no transition between them, it appears that their similarities are due to recent adaption and I have come to the conclusion that the Estrildinae have probably evolved independently from the Sporopipinae, just as have the Viduinae and the Ploceinae.

I hardly dare to suggest here that the very peculiar Celebean bird *Scissirostrum dubium* may prove to be related to the Estrildinae. This curious species, with its large pale yellow bill, its gray dress, brightened by shiny crimson on the rump and upper tail-coverts, and its pointed tail, is probably not a true starling, as has been generally accepted. In spite of its large size, it may show affinities to *Erythrura klein-*

*schmidtii* and to *Padda oryzivora*. Only a detailed anatomical and behavior study, and the examination of nestlings, may solve the question. But live specimens in my aviaries at Clères originated in my mind the possibility of their distant relationship to the Ploceidae. *Scissirostrum* may be a relict of forms which at some time stood between the weavers and the starlings. I am inclined to think that the Ploceidae are really nearer to the Sturnidae than to the Fringillidae, and their nesting habits indicate it. Nests placed in holes are less different from covered nests than the latter are from open, cup-shaped ones.<sup>1</sup> The same suggestion can perhaps even be made for another very peculiar Celebean species: *Enodes erythrophrys*, a still more aberrant bird.

Within the three major divisions indicated above, Estrildinae form very closely allied and rather poorly defined groups and the discrimination of genera, subgenera and species is not easy.

Considering that the presence of a well developed first primary is a primitive character, existing in the ancestral Sporopipinae, it is obvious that the two genera *Clytospiza* and *Spermophaga* represent the most primitive of Estrildinae. Consequently, the waxbill group is also the most primitive of the subfamily.

*Clytospiza* being much more generalized than *Spermophaga*, I consider it as the central nucleus of the whole subfamily. It contains three species, considerably different, but clearly related generically, and in turn each species is linked by some characters to other genera.

*Clytospiza monteiri* is gray above, reddish-brown mottled or spotted with white below, with crimson upper tail-coverts. The male has a triangular crimson patch on the throat. The beak is relatively long and curved, the tail rather short. The slender-billed, short-tailed genera *Nigrita*, *Parmopila* and *Pytilia* are linked to it, but they all have a short first primary.

*Clytospiza dybowskii* has a slightly thicker bill, still rather long; it is blackish-gray, with a crimson back and a black abdomen spotted with white. It is certainly related to the large-billed, red-and-black males, red-and-gray females of *Spermophaga*, the only other genus to retain a large first primary, and whose female has a white-spotted abdomen. It is close to the genus *Hypargos*, which differs practically only in its short first primary. It is also not far from the unspotted, olive or gray genus *Cryptospiza*, which has a crimson back and a thicker bill, and which in turn leads to the huge-billed *Pirenestes*.

<sup>1</sup> Under the artificial conditions of captivity, birds building normally domed nests usually take readily to nesting in boxes and hollow logs. Some starlings (*Spreo* and *Acridotheres*) build domed nests.



TEXT-FIG. 1. Relationship of the Estrildinae.

The third species, *C. cinereovinacea*, has a longer tail and a small bill. But for its long first primary, it would be a true *Estrilda*. In its dark gray plumage with dark crimson lower back and upper tail-coverts, and its crimson flanks, minutely spotted with white, it resembles closely the members of the subgenus *Lagonosticta*. The large genus *Estrilda* leads to the grass-finches: *Zonaeginthus* on one side, *Poephila* on the other. *Poephila* in turn leads to *Erythrura* through *P. gouldiae*, and through *P. modesta*, to the mannikins: *Padda*, *Amadina* and *Lonchura*.

As we shall see further on, some of these genera can be conveniently divided into subgenera on less important characters. The accompanying diagram shows the natural relationship of these different groups

of Estrildinae, which cannot be explained in a linear sequence.

We shall now study the different genera, subgenera and species, much as we have done before in "A revision of the genera and species of the family *Pycnonotidae*."<sup>12</sup> I shall not attempt to review critically all the subspecies, confining my remarks to interesting facts involving certain races and to the grouping of forms within a species. The sequence adopted below is perforce partly artificial, and as I have just remarked, only a diagram can give a proper idea of relationships.

In the present study, the numbers of genera and species have been reduced to 15 and 108 respectively. The numbers quoted in the *Systema Avium Aethiopicarum*, by W.

<sup>2</sup> *Zoologica*, Vol. XXVII 1943, pp. 17-28.

L. Sclater, the Fauna of British India, by E. C. Stuart Baker, the Handlist of Malaysian Birds, by F. N. Chasen, and the Systema Avium Australasiarum, by G. Mathews, amount to 50 genera and 137 species. Those quoted in two or more of the above works have been counted as one, and all known genera and species are included in these lists.

In reducing the number of genera, I have strictly followed the indications of the important characters mentioned earlier. Less

important ones have been considered for subgeneric distinctions, numbering 11. I have incorporated as subspecies of the same species forms which differ only in degree from one another, whether in proportions or in colors, and which replace one another geographically. I have kept as separate species all those geographical representatives whose color pattern is sufficiently and truly different, indicating superspecies relationships whenever necessary, following here the lines of my previous revisions.

## A. THE WAXBILLS (ESTRILDAE).

### I. GENUS *Spermophaga*.

Swainson, 1837. Type: *Spermophaga haematina*.

Size large.

Bill large and thick, bluish-gray and orange; both mandibles convex. Wing much rounded; 1st primary large, longer than one-half of 2nd, which is shorter than 3d and 10th; 4th, 5th, 6th and 7th longest and subequal. Tail moderate, broad and rounded, shorter than wing. Plumage of males black and red; females dark gray and red with abdomen gray-spotted all over with large terminal white dots.

Live in pairs in forest thickets.

1. *S. poliogenys*. Grant's Blue-billed Weaver. Belgian Congo.
2. *S. ruficapilla*. Red-headed Blue-billed Weaver. C. Africa, from Belgian Congo and Angola to Kenya and Tanganyika.
3. *S. haematina*. West African Blue-billed Weaver. West Africa, from Gambia to Portuguese and Belgian Congo.

### II. GENUS *Clytospiza*.

Shelley, 1896. Type: *Pytelia monteiri*.

Size medium.

Bill moderate and variable in length as in *Estrilda*. Wing much rounded; 1st primary large, reaching one-half or more of the 2d, which falls short of the 3d by about one-fifth; other primaries more or less subequal. Tail moderate, rounded and broad. Plumage variable, mostly gray, black, crimson or reddish-brown; upper tail-coverts always red; white spots on abdomen and sides of the breast. Sexes alike or slightly different.

Live in bushes, in open country.

1. *C. monteiri*. Brown Twin-Spot. Portuguese Congo, N. Angola and E. Cameroon to Barh-el-Ghazal, Upper White Nile and Uganda.
2. *C. dybowskii*. Dusky Twin-Spot. N. Cameroon to Ubangi-Shari and Upper Uele.
3. *C. cinereovinacea*. Dusky Fire-finch. Angola and Belgian Congo.

Note: This genus can only be upheld on account of its very peculiar and primitive wing formula. But for that, *C. monteiri* and *C. dybowskii* could be referred to *Hypargos*, and *C. cinereovinacea* to *Estrilda*. However, the significance of their long first primary cannot be ignored.

### III. GENUS *Hypargos*.

Reichenbach, 1863. Type: *Spermophaga margaritata*.

Size medium.

Bill rather long and strong. Wing variable; 1st primary minute; tail broad, rounded, moderate or short. Plumage brownish or greenish above; breast and upper tail-coverts crimson, orange or yellowish; flank feathers with large round twin spots, white or pale pink. Sexes different.

Live in thick bushes, in open country.

#### Subgenus *Hypargos*.

Tail longer; wing very round, 2d primary much shorter than 3d; 4th and 5th longer. Bill thicker, culmen more curved.

1. *H. niveoguttatus*. Rosy Twin-Spot. Portuguese East Africa (Inhambane).
2. *H. margaritatus*. Peter's Twin Spot. Kenya, Tanganyika and Nyassaland to Portuguese East Africa, Mashanoland, N. Rhodesia and Katanga.

#### Subgenus *Mandingoa*.

Hartert, 1919. Type: *Estrilda nitidula*.

Bill slightly thinner and straighter. Tail much shorter. Wing sharper, 2d and 3d primaries subequal and longest, in contrast to *Hypargos*.

3. *H. nitidulus*. Green-backed Twin-Spot. Sierra Leone to Natal.

### IV. GENUS *Cryptospiza*.

Salvadori, 1884. Type: *Pytelia reichenowi*.

Size medium to large.

Bill stout and thick, culmen curved. Wing rounded; 1st primary minute, 2d shorter than 3d; 4th and 5th longest. Tail short and

broad, rounded. Legs rather long and strong. Plumage gray, brown or olive, the back and upper tail-coverts crimson. No spots. Sexes alike, or nearly so.

Live in forest, at high altitude.

1. *C. shelleyi*. Shelley's Crimson-wing. Ruwenzori and Kivu mountains.
2. *C. salvadorii*. Salvadori's Crimson-wing. Mountains of E. Africa to Ruwenzori.
3. *C. reichenowi*. Red-eyed Crimson-wing. Cameroon Highlands to Ruwenzori, Kivu and Uluru Mts.; Fernando-Po.
4. *C. jacksoni*. Dusky Crimson-wing. Ruwenzori and Kivu Mts.

*Note:* *Cryptospiza* are forest birds of the high altitudes of Central Africa. *C. shelleyi* differs considerably in size, bill and color pattern, while the other three are more closely related. Since all of them are found together on Ruwenzori and other mountains, they must constitute separate species.

#### V. GENUS *Pirenestes*.

Swainson, 1837. Type: *Pirenestes sanguineus*.

Size large, but variable, even within the same species.

Bill large and very stout, rather short and pointed, of a very peculiar shape; culmen and sides nearly straight. Wing moderately rounded; 1st primary minute; 2d equal to 7th; 4th and 5th longest. Tail rounded and moderate. Legs rather long. Plumage black and red, or brown and red. Throat and upper breast, tail and upper coverts always bright crimson. Sexes different or almost alike.

Live in swamps and paddy fields surrounded by trees and bushes, forest clearings and edges.

1. *P. minor*. Eastern Seed-cracker. East Africa, from Nyassaland and Tanganyika to Mozambique.
2. *P. sanguineus*. Crimson Seed-cracker. West Africa, from Senegal to Liberia.
3. *P. ostrinus*. Black-bellied Seed-cracker. West Africa, from Togoland to Angola, east to Uganda.

#### VI. GENUS *Nigrita*.

Strickland, 1842. Type: *Aethiops canicapilla*.

Size large to small.

Bill long and slender, flattened at the nostrils. Wing rather sharp; 1st primary minute; 2d slightly shorter than 5th; 3d and 4th longest. Tail broad and rounded. Legs rather short and weak. Plumage variable, upper and underparts always of contrasting colors, never with bright hues and confined to black, gray, chestnut, brown and white. Sexes alike or only slightly different.

Live usually in forests, along water courses, on trees, and often feed on the pulp of oil-palm nuts, fruit and insects.

1. *N. canicapilla*. Gray-headed Negro-finch. From Sierra Leone to Angola, east to Kenya, Uganda and Tanganyika.
2. *N. luteifrons*. Pale-fronted Negro-finch. West Africa, from S. Nigeria to E. Belgian Congo, and Fernando-Po.
3. *N. bicolor*. Chestnut-breasted Negro-finch. From Portuguese Guinea to Gaboon, east to Belgian Congo and Uganda.
4. *N. fusconota*. White-breasted Negro-finch. From Gold Coast to Uganda; Fernando-Po.

*Note:* The Negro-finches are aberrant waxbills, whose slender bill is an adaptation to a diet of soft pulp and insects. But they are true waxbills in their nesting habits and the domino-marked palate of their chicks, showing five black spots.

#### VII. GENUS *Parmoptila*.

Cassin, 1859. Type: *Parmoptila woodhousei*.

Size small.

Bill very slender and deeply depressed at the nostrils. Wing slightly more rounded than in *Nigrita*; 3d, 4th and 5th primaries subequal. Plumage brown above; throat reddish-brown; underparts freckled or laced olive, brown, white or plain reddish-brown, according to race and sex.

Habits similar to *Nigrita*. Live on trees and feed on insects and nut pulp.

1. *P. woodhousei*. Flower-pecker Finch. West Africa, from Gold Coast to Angola and Belgian Congo.

*Note:* Very aberrant by reason of its thin bill, *Parmoptila* has the characteristic nesting habits and domino palate in nestlings of the true waxbills. Its connection with *Clytospiza monteiri*, if not very strong, is more visible than in *Nigrita*. All the forms seem to be subspecies of the same species. The fact that the male *P. w. jamesoni* is plain chestnut-red below and has the whole fore part of the crown crimson is only a difference in degree of pigmentation and does not warrant specific division. The female *jamesoni* and both sexes in other forms are very similar.

#### VIII. GENUS *Pytilia*.

Swainson, 1837. Type: *Pytilia phoenicoptera*.

Size medium.

Bill rather long and pointed; culmen slightly curved and compressed at the sides near the end. Wing rather sharp; 1st primary minute; 2d, equal to 6th, compressed,



pointed near the tip and cut away; 3d, 4th and 5th the longest. Tail short and slightly rounded. Feet moderate. Palate markings of nestlings reduced to one spot or none at all. Plumage barred or freckled with white below; tail-coverts and tail red.

Live in bushes in open, dry country.

1. *P. melba*. Melba Finch. Ethiopian region, from Senegal, Abyssinia and Erythrea to Natal and Damaraland.
2. *P. afra*. Red-faced Finch. From Ivory Coast to Abyssinia south to Beira, N. Rhodesia and Angola.
3. *P. phoenicoptera*. Aurora Finch. Senegal to Gold Coast, east to Abyssinia, Egyptian Sudan and N. W. Uganda.

*Note*: *P. hypogrammica* is evidently the western representative of *P. afra*. Their differences are only of degree and of sub-specific importance. *P. hypogrammica* has less yellow pigment, and the result is that its underparts are gray, instead of gray strongly suffused with olive yellow as in *afra*; its wings golden olive, instead of coppery orange; but otherwise both forms are entirely similar, except for the bill, which is black in *hypogrammica* and red in *afra*. The same state of things is found in the species *phoenicoptera*: the eastern race *lineata* has a red bill, while the western birds, *emini* and *phoenicoptera*, have it black. *P. lopezi* is either a color phase or a local race of *P. afra*.

### IX. GENUS *Estrilda*.<sup>3</sup>

Swainson, 1827. Type: *Loxia astrild*.

Size medium to very small.

Bill moderate or short, variable; culmen slightly curved to nearly straight. Wing moderately rounded and slightly variable; 1st primary minute or very small; 2d and 5th about equal; 3d and 4th longest, but not greatly so, and sometimes subequal with 2d and 5th. Tail graduated and long to rounded and short. Legs moderate. Plumage bright, sometimes cross-barred, but never spotted with large twin dots on the feathers of the underparts. Sexes similar or different.

Live usually in open grass and bush country, marshes, outskirts of woods and clearings, or near cultivation.

#### Subgenus *Lagonosticta*.

Cabanis, 1851. Type: *Fringilla rubricata*.

Bill rather long and compressed laterally near the tip; culmen slightly curved. Wing rounded, 2d primary pointed and cut away in three species. Tail broad and rounded. Plumage brown or gray, marked with black and different shades of crimson and pink.

<sup>3</sup> For taxonomic remarks on *Estrilda*, see Wolters, *Orn. Monatsb.*, Berlin, 1939 pp. 33-37.

Upper tail-coverts always red, except in *A. rufopicta harterti*. Sides with minute white spots, except in one species (*E. rara*). Sexes different with the exception of two species (*rufopicta*, *coerulescens*). Live often in villages or near cultivation, but also in the brush. They are not gregarious.

1. *E. rufopicta*. Brown Fire-finch. Senegal, east to the Upper Nile, south to N. Angola, N. Rhodesia, Katanga and Lake Tanganyika.

2. *E. senegala*. Red-billed Fire-finch. The greater part of the Ethiopian region.

3. *E. jamesoni*. Jameson's Fire-finch. N. Transvaal, Bechuanaland and Metabele country to the Zambesi; Angola; coastal Kenya.

4. *E. rubricata*. Dark Fire-finch. The greater part of the Ethiopian region, except the southwest.

5. *E. rara*. Black-bellied Fire-finch. Cameroon and Nigeria to Upper White Nile.

6. *E. larvata*. Masked Fire-finch. Senegal to Cameroon, east to Abyssinia, Bahr-el-Ghazal and N. Uganda.

7. *E. coerulescens*. Lavender Finch. West and South Africa.

*Note*: The lack of very great significance of the pointed and notched second primary is illustrated by the fact that three species show it (*senegala*, *rubricata*, *larvata*) while three others do not (*rufopicta*, *coerulescens* and *jamesoni*), and *rara* is intermediate. But I think it is of specific value, and therefore I separate *jamesoni*, *benguellensis* (= *ansorgei*) and *teruensis* from *rubricata*. On the other hand, as *landanae*, which shows it, does not overlap geographically with any form I ascribe to *rubricata*, I consider it a subspecies of the latter species; the rather special coloration of its bill does not deserve specific distinction.

I consider *rufopicta* and *harterti* (= *nitidula*) as conspecific. The fact that *harterti* lacks red on the upper tail-coverts and rump, is altogether paler, has less pink and larger white spots on the breast, does not seem to warrant specific rank; it is only a difference in degree in the red pigmentation.

It is curious that *larvata* has been so often removed from the *Lagonosticta* group, as it shows distinctly all its essential characters; *vinacea* and *nigricollis* are obviously subspecies of *larvata*. *E. coerulescens* is the nearest to the subgenus *Estrilda*; it includes the southern black-tailed races often separated as *E. perreini*.

#### Subgenus *Estrilda*.

Bill variable, but shorter than in *Lagonosticta*. Wing varying within the limits of the genus; second primary never cut away. Tail narrow and long (*granatina* and *erythronotos*) to short and moderately

broad (*melanotis* and *shellei*). Plumage varied, sometimes finely lined transversely, never coarsely barred below, nor minutely spotted on the sides of the body. Always some bright crimson, blue, mauve or yellow on the face or on the upper tail-coverts, or on both. Sexes generally alike, sometimes slightly different.

Live in open country, clearings and cultivation, usually in flocks.

8. *E. cyanocephala*. Blue-headed Waxbill. Kenya, from Kilimanjaro to N. Guaso Nyiro.

9. *E. angolensis*. Cordon-bleu Waxbill. The greater part of the Ethiopian region.

10. *E. ianthinogaster*. Purple-bellied Waxbill. N. E. Africa, from Abyssinia and Somaliland to Kenya, N. Tanganyika and N. Uganda.

11. *E. granatina*. Violet-eared Waxbill. S. W. and South Africa, from Angola to the Transvaal, the Orange Free State and Griqualand West.

12. *E. erythronotos*. Black-cheeked Waxbill. East and South Africa, from S. Abyssinia and Somaliland to Damaraland, Great Namaqualand, W. Matabeleland and the Transvaal.

13. *E. astrild*. St. Helena Waxbill. The greater part of the Ethiopian region, south of Sierra Leone and the Egyptian Sudan.

14. *E. rhodopyga*. Crimson-rumped Waxbill. East and N. E. Africa.

15. *E. troglodytes*. Gray Waxbill. West Africa, from Senegal to N. Cameroon and east to the Upper Nile and the Shari rivers; S. W. Arabia.

16. *E. temporalis*. Sidney Waxbill. E. Australia.

17. *E. melpoda*. Orange-cheeked Waxbill. West and East Africa, from Senegal to Angola, east to Abyssinia and N. Rhodesia.

18. *E. atricapilla*. Black-headed Waxbill. Cameroon and Belgian Congo; east to central Kenya.

19. *E. nonnula*. Black-crowned Waxbill. Fernando-Po and Cameroon, east to W. Kenya.

20. *E. melanotis*. Dufresne's Waxbill. East and South Africa, from Abyssinia to the Cape Colony.

21. *E. shelleyi*. Olive-backed Waxbill. Fernando-Po, Cameroon, Uganda and Belgian Congo.

22. *E. capistrata*. Gray-headed Waxbill. West Africa from Gambia to Cameroon, east to Barh-el-Ghazal and Lake Albert.

Note: I find it impossible to draw a line between the different species of the subgenus *Estrilda*. Changes in coloration, size and shape of the bill, length of the tail or wing formula are so gradual and indepen-

dent of one another, that I cannot recognize even as subgenera *Uraeginthus*, *Coccopygia* and *Nesocharis*. *E. erythronotos* has proportionally as long a tail as any "*Uraeginthus*." The bill of "*Coccopygia*" *melanotis* is neither thicker nor more curved than that of *E. melpoda* or *E. atricapilla*, nor more part-colored than in the latter species, and the shortness of its tail is of no more than specific value. The same applies to "*Nesocharis*" *shellei* and *N. capistrata*, and their special coloration is not more peculiar than that of several other species.

I have united specifically a number of forms usually so far considered separate species. It is now proved that *E. angolensis* and *E. bengala* replace one another geographically and intermediates have been found between them; I consider therefore the different forms of *E. bengala* as subspecies of *E. angolensis*, the oldest name. *E. cyanocephala* is a very close, but separate species, as it cohabits with forms of *E. angolensis*.

*E. charmosyna* is but a northern, pale, dry country form of *E. erythronotos*, with *delamerei* as a link. The latter does not coexist with *charmosyna* although they may both meet and interbreed on their boundary, a very normal state of things for two subspecies.

The Arabian waxbill, *E. rufibarba*, is better considered a race of *E. troglodytes*, of which it has the black rump, although it has the black bill of *E. rhodopyga*. *E. xanthophrys* and *E. nigriloris* are either color phases or subspecies of *troglodytes* and of *astrild*. *E. rhodopyga* is certainly close to *E. troglodytes*, but too different to be united.

The Australian *E. temporalis* is a typical waxbill in every way, intermediate on many sides between *E. troglodytes* and *E. melpoda*.

The western *E. melpoda* is undoubtedly conspecific with the eastern *E. paludicola*, which only differs in the absence of orange on the face, and in an increase in the pink on the abdomen, a variation in degree of pigmentation similar to that of the races of *E. melanotis*, which may or may not possess a black face and throat in the male. *E. roseicrista* is also a subspecies of *melpoda*.

*E. atricapilla* and *E. nonnula*, superficially similar, coexist over a large territory and constitute two separate species.

*E. melanotis* is very close to them, having only a shorter tail. In *E. quartinea*, both sexes have no black on the head and are similar to the female of *melanotis*, of which it is a subspecies.

*E. shelleyi* is a peculiar short-tailed species, gray, black and olive-yellow, found in mountain forests. I consider *E. ansorgei*



as a subspecies, notwithstanding its much thicker bill and slightly larger tail, as it is exactly alike in color pattern. Related to *shelleyi* is *E. capistrata*, a very distinct low-land bird, perhaps the most aberrant species of the whole group.

#### Subgenus **Amandava**.

Blyth, 1836. Type: *Fringilla amandava*.

Size small or very small.

Bill moderate and conical. Wing rather sharp; 2d to 5th primaries sub-equal. Tail rather short and rounded. Legs moderate; toes comparatively long and slender. Plumage variable: brown, olive, yellow, orange or red, with either coarse cross-barring on the sides and flanks, or white spots on the upperparts. Sexes different. Voice sweet.

Live in grass and bushes, in, or near marshes, paddy and sugar-cane fields.

24. *E. amandava*. Red Avadavat<sup>4</sup>. Ceylon, India, Burma, N. Tonkin, N. Siam, S. Yunnan, Cochinchina, Cambodia, Java, Bali, Lombok, Flores, Sumba, Timor.

25. *E. formosa*. Green Avadavat. Central India.

26. *E. subflava*. Orange breasted Wax-

bill. Greater part of the Ethiopian region, from Senegal, east to Kenya and Abyssinia, south to Natal and Angola.

#### Subgenus **Ortygospiza**.

Sundevall, 1850. Type: + *Fringilla polyzona* = *E. atricollis polyzona*.

Size small or very small.

Wing formula as in species of the subgenus *Amandava*, to which they are very closely related, differing only in their decidedly thicker bill, stronger and longer legs, shorter tail, louder voice, and in their much more terrestrial habits.

Live on the ground, in veld, meadows and marshes, among the grass.

27. *E. locustella*. Locust Finch. Central Africa.

28. *E. atricollis*. Quail Finch. The greater part of the Ethiopian region, from Senegal to Erythrea and South Africa.

*Note:* All forms of *E. atricollis* have bars on the breast, sides and flanks. Females of *E. locustella* have bars on the sides, and resemble very much *E. subflava*. But the crimson and black males have no barring, just like *E. amandava*. Those of the nominal race (*locustella*) have white spots above like males of *E. amandava*, while males of *E. l. uelensis* have none.

<sup>4</sup> See revision: J. Delacour, *L'Oiseau*, 1935, pp. 379-384.

## B. THE GRASSFINCHES (ERYTHRURAE).<sup>5</sup>

### X. GENUS **Zonaeginthus**.

Cabanis, 1851. Type: *Loxia bella*.

Size medium.

Bill moderate to long, conical; mandibles almost straight. Legs and toes moderate to strong. Wing moderately rounded, Tail rather short and rounded. Plumage brown above, rump and upper tail-coverts crimson. Sexes alike or nearly so.

Live in open country near the ground, in the brush.

#### Subgenus **Zonaeginthus**.

Size smaller.

Legs moderate. Wing sharper; primaries straight, rather stiff and narrow; 2d primary the longest and subequal with 3rd and 4th and 5th. Sides and flanks black; boldly spotted or striped with white.

1. *Z. pictus*. Painted Finch. Central and N. W. Australia.

2. *Z. oculatus*. Red-eared Fire-tail Finch. S. W. Australia.

3. *Z. bellus*. Fire-tail Finch. E. Australia and Tasmania.

4. *Z. guttatus*. Diamond Sparrow. E. Australia.

#### Subgenus **Oreostruthus**.

DeVis, 1896. Type: *Oreospiza fuliginosa*.

Size larger.

Legs and toes long and strong. Wing well rounded; 2nd primary much shorter than 3rd, which in turn is much shorter than 4th and 5th. Primaries broad and soft, slightly pointed and curved outwards. Underparts brown freckled with crimson.

5. *Z. fuliginosus*. Crimson-bellied Mountain Finch. New Guinea, above 2,800 m.

*Note:* The connection between *Z. pictus* and the other species of this genus has been often overlooked, and too much stress has been laid on its long, thin bill, compared to the shorter, conical beaks of the others. This is merely a difference in degree, and they all have rather pointed bills. General proportions and color pattern are in fact quite consistent in the four species.

Although evidently related to the other four, *Z. fuliginosus* deserves subgeneric distinction on account of its special wing formula, very large feet and legs and peculiar coloration.

<sup>5</sup> For interesting information on Australian grass finches, see N. W. Cayley: Australian Finches in Bush and Aviary, Sydney, 1932.

According to H. Sedley (in litt.), nestlings of *Z. pictus* have three spots, with two short lines below, on the palate.

### XI. GENUS *Poephila*.

Gould, 1842. Type: *Amadina acuticauda*.

Size medium.

Bill rather thick, culmen slightly curved and swollen at the base. Wing moderately rounded; 1st primary minute; 2nd slightly or hardly shorter than 3rd; 4th and 5th long. Tail variable. Legs moderate, toes fairly long. Plumage extremely elaborate, varied and diversified. Sexes alike or different.

Live in open country dotted with trees, long grass and bushes.

#### Subgenus *Neochmia*.

Gray, 1849. Type: *Fringilla phaeton*.

Tail rounded or graduated, central rectrices never ending in a sharp point. Plumage pattern complicated and elaborate, with always a great deal of spotting or barring.

1. *P. phaeton*. Crimson Finch. N. Australia and S. New Guinea.

2. *P. ruficauda*. Red-tailed Finch. N. and E. Australia.

3. *P. guttata*. Zebra Finch. Australia, Timor and Flores.

4. *P. bichenovi*. Owl Finch. N. and E. Australia.

5. *P. modesta*. Cherry Finch. E. Australia.

#### Subgenus *Poephila*.

Tail rounded or graduated, the two central rectrices always ending in a rachial point, of variable length. Plumage pattern bold, made of large patches of different colors, without bars or spots. Always a black patch on the throat.

6. *P. cincta*. Parson Finch. E. Australia.

7. *P. acuticauda*. Shaft-tailed Finch. N. and N. W. Australia.

8. *P. personata*. Masked Finch. N. Australia.

9. *P. gouldiae*. Gouldian Finch. N. Australia.

*Notes:* This genus is extremely difficult to arrange, as many of the species included are highly specialized in color pattern and general proportions, and no intermediates exist between them. That is the reason why so many monotypic, and in my judgment utterly unnecessary genera, have been created for them.

Besides the coloration, the length and shape of the tail differ much. But the bill is fairly uniform. The wing formula varies a little, the 2d primary being clearly shorter

than the 3d in *P. phaeton*, slightly so in *P. acuticauda* and *P. personata*, and subequal to 3d, 4th and 5th in all the other species. But the general structure of the wing is the same, and variations are too slight to warrant even subgeneric distinction.

In the subgenus *Neochmia*, *P. evangelinae* is nothing but a subspecies of *P. phaeton*; there is no proof whatever of their overlapping on Cape York Peninsula.

*P. castanotis* from Australia, and *P. guttata* from Timor and Flores, are decidedly conspecific; *guttata* is the oldest name for the species.

*P. modesta* resembles superficially *Lonchura malabarica*, but I am convinced that there is no real close relationship between them. When we know the palate markings of this species, we shall be able to finally decide on this point.

In the nominal subgenus, *P. cincta* and *P. acuticauda* constitute a superspecies.

*P. gouldiae* has three color phases: black, red and yellow-headed, which bear no relation to geographical distribution. The so-called yellow-headed form is very rare and the color of its head is really a dull cinnabar orange.

The intermediate position of the genus is further emphasized by the palate markings of the nestlings of the different species. *P. phaeton* (Rand), *P. guttata*, *P. bichenovi*, *P. gouldiae* show distinct spots, while *P. cincta*, *P. acuticauda*, *P. personata* have short lines, but these are not horseshoe-like in shape (Neunzig).

### XII. GENUS *Erythrura*.

Swainson, 1837. Type: *Loxia prasina*.

Size medium.

Bill strong, often long. Legs and feet strong. Wing rather sharp; 1st primary minute; 2d, 3d, 4th, 5th, subequal (2nd slightly shorter in *E. kleinschmidti*). General color grass green. Sexes alike or slightly different. Low metallic voice.

Live mostly in bamboo forests and groves.

#### Subgenus *Reichenowia*.

Poche, 1904. Type: *Chlorura hyperhythra*.

Bill black, moderate, pointed and compressed near tip. Tail rounded; rump and upper tail-coverts green. Sexes similar.

1. *E. hyperhythra*. Green-tailed Parrotfinch. Malay Peninsula, Sumatra, Borneo, Java, Lesser Sunda Islands, Philippines and Celebes (mountains).

#### Subgenus *Erythrura*.

Bill strong and black, compressed near the tip. Tail pointed and graduated, red as well as its upper coverts. Sexes similar or slightly different.

2. *E. viridifacies*. Manilla Parrot-finch. Luzon (Philippine Islands).

3. *E. prasina*. Pintail Nonpareil. N. Laos, Malay Peninsula, Sumatra, Java and Borneo.

4. *E. tricolor*. Tricolored Parrot-finch. Timor, South West Islands and Tenimber Islands.

5. *E. trichroa*. Blue-faced Parrot-finch. New Guinea, N. Australia (Cape York), Celebes, Moluccas, Bismarck Archipelago, Micronesia, Solomons, New Hebrides and Loyalty Islands.

6. *E. papuana*. Papuan Parrot-finch. New Guinea (mountains).

7. *E. psittacea*. Red-headed Parrot-finch. New Caledonia.

8. *E. cyanovirens*. Blue-bellied Parrot-finch. Samoa, Fiji and New Hebrides.

#### Subgenus **Ramphostruthus**.

Mayr, 1931. Type: *Amblyura kleinschmidti*.

Bill strong and long, creamy white, not compressed. Tail rounded, crimson. Wing more rounded; forehead velvety and bluish-black. Sexes similar.

9. *E. kleinschmidti*. Black-faced Parrot-finch. Viti Levu (Fiji).

Note: The parrot-finches form an isolated group, with no great affinities to other Estrildinae. The green upper parts of *P. gouldiae* do not seem to imply close relationship. It is probably an ancient, rather primitive genus, adapted to life among bamboos. But the domino palate pattern of young *E. psittacea*, figured by Sarasin (Die Vogel Neu-Caledonia, 1913), leaves no doubt as to their place among the grassfinches.

### C. THE MANNIKINS (AMADINAE).

#### XIII. GENUS **Padda**.

Reichenbach, 1850. Type: *Loxia oryzivora*.

Size large.

Bill very large, both mandibles slightly convex. Legs strong, toes long and fleshy. Wing rather sharp; 1st primary minute; 2d, 3d, 4th and 5th subequal. Tail rounded, black. Plumage gray or brown; head and throat black, with large white cheek patches. Sexes similar.

Live in open and cultivated country.

1. *P. oryzivora*. Java Sparrow. Java and Bali (elsewhere, probably introduced).

2. *P. fuscata*. Timor Sparrow. Timor and Saman Island.

Note: According to Sushkin, the genus *Padda* is a well defined one because of its anatomical peculiarities. Its general appearance, life habits and color pattern are certainly in accord with this view.

#### XIV. GENUS **Amadina**.

Swainson, 1827. Type: *Loxia fasciata*.

Size large to medium.

Bill short and stout, swollen at base. Wing rather sharp; 1st primary minute; 2d, 3d, 4th and 5th subequal. Tail short and rounded. Legs moderate, toes slender. Plumage pale rufous brown, many feathers barred with black, or spotted; red on head or throat in males. Sexes different.

Live in dry open bushy country.

1. *A. fasciata*. Cut-throat Finch. West, Central and East Africa, south to N. Rhodesia.

2. *A. erythrocephala*. Red-headed Finch. South Africa north to Angola, S. Rhodesia and the Transvaal.

Note: In its color pattern, sexual differences and the dress of juveniles, *Amadina* is decidedly different from *Lonchura*. The large blotches on the nestlings' palate and tongue are also very peculiar.

#### XV. GENUS **Lonchura**.

Sykes, 1832. Type: *Fringilla nisoria* (subspecies of *punctulata*).

Size medium to small.

Bill stout, swollen at the base. Wing rather sharp; 1st primary minute, 2d, 3d, 4th and 5th subequal. Tail short or moderate. Legs rather short, toes long. Plumage varied, but without bright colors. Sexes similar or very nearly so.

Live in open country of bushes and tall grass, edges of forest and clearings, gardens and cultivated fields.

#### Subgenus **Heteromunia**.

Mathews, 1913. Type: *Amadina pectoralis*.

Size moderate.

Bill moderately long and thick, silver gray. Tail short and rounded; no ornamental decomposed fringes on rump or tail feathers. General color pale rufous brown and gray, with a large black patch on the cheeks and throat, small white spots on the wings and sides of body and a white band on the breast, made of the broad white tips of the feathers.

1. *L. pectoralis*. Pectoral Finch. Northern Australia.

Note: This species constitutes in many ways an intermediate between the grassfinches and the mannikins. It has the general aspect and shape of the latter, particularly those of the subgenus *Munia*,

but its elaborate spotting seems to be nearer to the pattern of the grassfinches of the subgenus *Neochmia*. Moreover, according to Cayley (*op. cit.*, p. 102), its display is very close to those of *P. phaeton* and of *P. ruficauda*. But the mouth markings of the nestlings are those of the mannikins, according to Mr. Henry Sedley, who writes from Los Angeles on June 1, 1943, as follows: "Two of the young pectoral finches, for some reason, have left the nest, much too soon. I caught one and examined it carefully. At the corners of its mouth it has a blue line extending along both upper and lower mandibles for possibly a sixteenth of an inch. The line on the roof of the mouth is unbroken and is in the horse-shoe shape." The systematic position of the pectoral finch is therefore evident, and it really belongs to the genus *Lonchura*. Its peculiarities, however, warrant its separation in a special subgenus.

#### Subgenus **Euodice**.

Reichenbach, 1862. Type: *Loxia cantans*.

Size medium.

Bill thick and short, silver gray. Head small for the genus. Tail comparatively long, black or purplish, rounded, the two central feathers elongated or not. General color pale rufous brown. No ornamental decomposed fringes on rump or tail feathers.

2. *L. malabarica*. Common Silver-bill. Tropical N. W., Central and N. E. Africa, S. Arabia, Persia, Afghanistan, Baluchistan, India and Ceylon.

3. *L. griseicapilla*. Gray-headed Silver-bill. (Nomen novum for *L. caniceps*, *Pytilia caniceps* Reichenow, 1879, preoccupied by *L. (Munia) caniceps* (Salvadori), 1876). S. Kenya, Uganda and Tanganyika.

*Note*: The African and Asiatic common silver-bills are undoubtedly conspecific. The gray-headed species is conspicuously different in the color of its head and in the shape of its almost square tail, but in habits and otherwise, it is very close to *malabarica*, which it replaces geographically.

The three above species are closer to the grassfinches than all other *Lonchura*, being more active, lighter in build, and having a shriller voice. The nestling has the continuous black palate mark of the mannikins in *Euodice* (Bates, *Ibis*, 1934, p. 705).

#### Subgenus **Lonchura**.

Size medium to small.

Bill stout, but variable in length, gray or black, dull red and black in *L. nana*. Tail rather short, rounded or pointed; upper tail-coverts little or not at all decomposed, sometimes bordered with yellow; rump often mottled gray and white, pure yellow in *tristissima* and *leucosticta*. Plumage

elaborate, marked, spotted or lined with black, white, gray or brown, exceptionally mainly brown or black.

4. *L. fringilloides*. Magpie Mannikin. The greater part of the Ethiopian region.

5. *L. bicolor*. Black-breasted Mannikin. The Ethiopian region south to Angola, the Belgian Congo and Natal.

6. *L. cucullata*. Bronze Mannikin. The greater part of the Ethiopian region.

7. *L. leucogastroides*. Javanese Mannikin. S. Sumatra, Java, Bali and Lombok.

8. *L. molucca*. Moluccan Mannikin. Flores, Sumba, Sumbawa, Kalao, Kalao-Tua, Celebes and Moluccas.

9. *L. fuscans*. Dusky Mannikin. Borneo, Banguay and Natuna Islands.

10. *L. striata*. Striated Mannikin. Ceylon, India, Burma, Siam, S. China, Indochina, Andaman and Nicobar Islands, Malay Peninsula, Sumatra.

11. *L. leucogastra*. White-breasted Mannikin. Malay Peninsula, Sumatra, Borneo, Philippines.

12. *L. kalaarti*. Jerdon's Mannikin. Ceylon and S. W. India.

13. *L. tristissima*. Yellow-rumped Mannikin. New Guinea.

14. *L. leucosticta*. White-spotted Mannikin. S. New Guinea.

15. *L. punctulata*. Nutmeg Mannikin. Ceylon, India, Burma, S. China, Siam, Indochina, Hainan, Formosa, Philippines, Malay Peninsula, Sumatra, Java, Bali, Lesser Sunda Islands, Celebes.

16. *L. nana*. Bib Finch. Madagascar and Mayotte Island.

*Note*: The species included in the subgenus *Lonchura* are certainly not so highly specialized as those of the subgenus *Munia*. But the two subgenera are so gradually linked together that generic separation is impossible. In the proportions of their beak or feet, in the ornamentation of their rump or tail feathers, the species *nana*, *leucogastra*, *kalaarti*, *tristissima*, *leucosticta* and *punctulata* provide a transition between the more generalized forms and the different species placed in the subgenus *Munia*.

*L. bicolor*, *L. nigriceps* and their races are conspecific.

The African species are primitive, but not more so than some of the Indo-Malayan ones, from which they cannot be separated subgenerically. Indeed *L. cucullata* is very similar to *L. leucogastroides* and *L. molucca* is also closely related.

The Malaysian *L. leucogastra* is entirely different, and conspecific with the Philipinian *L. everetti*, both having the upperparts with pale rachial lines, and largely yellow rectrices.

*L. jerdoni*, from S. W. India, is obviously a subspecies of *L. kalaarti*, from Ceylon, differing only in its plain rufous, instead of mottled, abdomen; its upper tail-coverts are yellow.

*L. tristissima*, with its races *hypomelana* and *calaminoros*, are extremely close to *L. leucosticta*, all having a yellow rump. But both are found together on the Noord River, in southern New Guinea, a fact necessitating specific distinction.

*L. nana*, from Madagascar, is quite a distinct bird, approaching *Euodice* in general coloration, but its black throat, red and black bill and pink legs are peculiar; because of its habits and of its yellow upper tail-coverts, however, I believe that it is a member of the subgenus *Lonchura*.

In *L. punctulata*, which has numerous subspecies, variations in the mottling of the underparts and in the size and intensity of the yellow fringes to the tail feathers are considerable, but there is little gradual change connected with geographical distribution.

#### Subgenus **Munia**.

Hodgson, 1836. Type: *Loxia rubroniger* (= *L. ferruginosa atricapilla*).

Size medium.

Bill stout, silver gray. Head large. Body long. Toes very long. Tail short and pointed, with highly decomposed, ornamental and vividly colored fringes to rectrices and upper coverts, as also to the rump feathers. Upperparts chestnut, brown or black; underparts variable.

17. *L. quincticolor*. Five-colored Mannikin. Lesser Sunda Islands, from Lombok to Alor, Sumba, Timor and South West Islands.

18. *L. ferruginosa*. Chestnut Mannikin. Ceylon, India, Burma, Siam, S. China, Formosa, Hainan, Indochina, Malay, Peninsula, Sumatra, Java, Bali, Borneo, Philippines, Lombok, Flores and Celebes.

19. *L. grandis*. Great-billed Mannikin. New Guinea.

20. *L. forbesi*. Forbes' Mannikin. New Ireland.

21. *L. spectabilis*. White-bellied Mannikin. New Guinea and New Britain.

22. *L. nigerrima*. Black Mannikin. New Hanover and N. New Ireland.

23. *L. nevermanni*. Nevermann's Mannikin. S. New Guinea.

24. *L. maja*. Pale-headed Mannikin. Malay Peninsula, Sumatra and neighboring islands, Java, Bali, Lombok, Flores, Celebes, New Guinea and N. Australia.

25. *L. castaneothorax*. Chestnut-breasted Mannikin. Australia and New Guinea.

26. *L. teerinki*. Teerink's Mannikin. Central New Guinea.

27. *L. stygia*. Stresemann's Mannikin. S. New Guinea.

28. *L. monticola*. Southern Mountain Mannikin. S. E. New Guinea, above 2,800 metres.

29. *L. montana*. Junge's Mountain Mannikin. Central New Guinea, at 4,000 metres.

30. *L. melaena*. Parrot-billed Mannikin. New Britain.

*Note*: The numerous forms of this very highly specialized subgenus can be divided into several well marked superspecies and species.

*L. quincticolor* is quite distinct, but closely related to the next species.

The different forms, mostly chestnut and black, a few having some pure white on the head or on the underparts, but all with black chin, throat, upper breast and abdomen, and a moderate bill, can be referred to the species *ferruginosa*, the oldest name for the group, which includes *atricapilla*, *malacca*, *bruniceps* and *jagori*, and their races. *L. grandis*, with a much large bill and more black underneath, forms a superspecies with *ferruginosa*.

Another superspecies is composed of *L. spectabilis* (and its subspecies *L. s. mayri*), *L. forbesi*, *L. nevermanni* and *L. nigerrima* (with its subspecies *L. n. hunsteini*).

*L. maja* includes as subspecies all the pale-headed forms: *pallida*, *subcastanea*, *vana*, *caniceps*, *kumisi*, *strachleyana* and *flaviprymna*, which only differ in degree and replace one another geographically. There are lowland and mountain forms among them.

All the remaining forms, with elaborately marked underparts and head, compose a large superspecies: *L. castaneothorax* and its races, *ramsayi* (new name for *nigricaps*), *sharpei* and *uropygialis*; *L. teerinki* and *L. stygia*, which are better considered separate species on account of their darker and simpler pattern, but are nevertheless representatives of *L. castaneothorax*; *L. monticola* and *L. montana*, highly specialized and closely connected mountain forms, but different enough in pattern, which I rather reluctantly retain as two distinct species; and, in the end, the huge-billed, curiously colored *L. melaena*.

The very peculiar case of several specimens of *M. m. flaviprymna* has been mentioned by D. Seth-Smith (*Avicultural Magazine*, New Series, Vol. V., 1907, pp. 195-198) and by G. Mathews (*The Birds of Australia*, vol. XII, p. 203). The birds, apparently imported and wild caught, showed in subsequent molts, after well over a year in captivity, dark markings on the throat, breast and sides of the body, suggesting a transition between *flaviprymna* and *castaneothorax*. Seth-Smith did not think probable

that they could have been hybrids, as it took, in his opinion, too long a time for the dark feathers to appear. He suggested that *flaviprymna* was but a pale desert form of *castaneothorax*, and that a more humid environment had caused the dark feathers to appear. It is a very doubtful possibility, since a wild shot female in the American Museum, Rothschild collection, no. 721,473, Victoria River, 30th June, 1902, shows a gray crown and a dark brown-spotted throat just like the birds mentioned above. The possibility of a hybridization remains. *L. flaviprymna* and *L. castaneothorax* are respectively very close to representatives of two distinct species: *ramsayi* (*nigriceps* auctorum) and *caniceps*, which are found living together in S. E. New Guinea; it seems therefore most unlikely that they can be conspecific. At present, I prefer to refer *flaviprymna* to the species *maja*. But it remains difficult to explain the changes in the plumage of the birds observed by Seth-Smith.

N. W. Cayley (*op. cit.*, pp. 84-90) discusses this question very carefully; he also believes in the specific distinction of *castaneothorax* and *flaviprymna*. On p. 92, he quotes Mr. A. Ashton-Hansen, of Sidney, who has observed that the display and song of *flaviprymna* are unlike those of *castaneothorax*, but exactly similar to those of *L. maja*, a very strong argument in favor of the specific unity of all the pale-headed mannikins.

#### NOMENCLATURAL NOTES.

As a result of the suppression of several untenable generic names and of the inclusion of several species in wider genera, a few nomenclatural changes have become necessary:

1. *Estrilda rufopicta nitidula* (*Lagonosticta nitidula* Hartlaub, 1886) is preoccupied by *Estrilda nitidula* Hartlaub, 1865, now included in the genus *Hypargos*. As pointed out by Wolters, Orn. Monats, 1939, pp. 33-37, the next available name is *Estrilda rufopicta harterti* (*Hypargus harterti* Shelley, 1903).

2. *Estrilda jamesoni ansorgei* (*Lagonosticta rhodopareia ansorgei* Neumann, Bull. B. O. C., XXI, p. 58, 1908) and *Estrilda atricollis ansorgei* (*Ortygospiza ansorgei* Og. Grant, Bull. B. O. C., XXV, p. 84, 1910) are preoccupied by *Estrilda shelleyi ansorgei* (*Putelia ansorgei* Hartert, Bull. B. O. C., X, p. 26, 1899). I propose for the first the new name *Estrilda jamesoni benguellensis* and for the second, *Estrilda atricollis gambiensis*.

3. *Estrilda ianthinogaster ugandae* (*Gratinaria i. ugandae*, Van Someren, Bull. B. O. C. XL, p. 53, 1919) is preoccupied by *Estrilda angolensis ugandae* (*Uraeginthus bengalus ugandae* Zedlitz, Journal Orn.,

LIX, p. 606, 1911); I propose for it the new name *Estrilda ianthinogaster somereni*, if the subspecies is valid, which I am not now in a position to ascertain.

4. *Estrilda astrild nyanzae* Neumann, Journal. Orn., 1907, p. 596, is preoccupied by *Estrilda melanotis nyanzae* (*Neisna dufresneyi nyanzae* Neumann, Journal Orn., 1905, p. 350). The name *Estrilda astrild munzneri* Kothe, 1911, is available for this subspecies.

5. *Lonchura ferruginosa orientalis* (*Munia malacca orientalis* Stuart Baker, Bull. B. O. C., XLV, 1925, p. 58) is preoccupied by *Lonchura cantans orientalis* (*Aidemosyne orientalis* von Lorenz and Hellmayr, Orn. Monats., IX, p. 39, 1901). I propose for it the new name *Lonchura ferruginosa bakeri*.

6. *Lonchura caniceps* (*Pytilia caniceps* Reichenow, Orn. Centrall., IV, p. 139, 1879) is preoccupied by *Lonchura maja caniceps* (*Munia caniceps*, Salvadori, Ann. Mus. Civ. Genoa, IX, p. 38, 1876). I propose for it the new name *Lonchura griseicapilla*.

7. *Lonchura castaneothorax nigriceps* (*Donacola nigriceps* Ramsay, Proc. Linn. Soc. N.S.W.I., p. 392, 1877) is preoccupied by *Lonchura bicolor nigriceps* (*Spermestes nigriceps* Cassin, Proc. Acad. Nat. Sci. Philadelphia, 1852, p. 185). I propose for it the new name *Lonchura castaneothorax ramsayi*.

#### ALPHABETICAL LIST OF GENERIC NAMES.

In **bold face**, valid genera; in **SMALL CAPITALS**, subgenera; in *italics*, synonyms.

*Acalanthe* Reichenbach, 1862. (*E. psittacea*) = *Erythrura*.

*Aegintha* Cabanis, 1851. (*E. temporalis*) = *Estrilda*.

*Aethiops* Strickland, 1841. (*N. canicapilla*) = *Nigrita*.

*Aidemosyne* Reichenbach, 1862. (*P. modesta*) = *Poephila*.

*Alisteranus* Mathews, 1912. (*P. cincta*) = *Poephila*.

**Amadina** Swainson, 1827. (*A. fasciata*).

**AMANDAVA** Blyth, 1836. (*E. amandava*). Subgenus of *Estrilda*.

*Amaurestes* Reichenbach, 1862. (*L. fringilloides*) = *Lonchura*.

*Amblymura* Reichenbach, 1862. (*E. cyanovirens peali*) = *Erythrura*.

*Atopornis* Reichenow and Neumann, 1895. (*N. c. diabolica*) = *Nigrita*.

*Bathilda* Reichenbach, 1862. (*P. ruficauda*) = *Poephila*.

*Bichenoa* Moulton, 1923. (*P. bichenovi*) = *Poephila*.

*Brunhilda* Reichenbach, 1863. (*E. erythronotos*) = *Estrilda*.



- Cayleya* Iredale, 1929. (*Z. pictus*) = *Zonaeginthus*.
- Chloebea* Reichenbach, 1862. (*P. gouldiae*) = *Poephila*.
- Chlorestrilda* Shelley, 1905. (*E. shelleyi ansonae*) = *Estrilda*.
- Chloromunia* Mathews, 1923. (*E. trichroa macgillivrayi* = *sigillifera*) = *Erythrura*.
- Chlorura* Reichenbach, 1862. (*E. hyperhythra*) = *Erythrura*.
- Clytospiza** Shelley, 1890. (*C. monteiri*).
- Coccygia* Cabanis, 1861. (*E. melanotis*) = *Estrilda*.
- Cryptospiza** Salvadori, 1884. (*C. reichenowi*).
- Dermophrys* Hodgson, 1841. (*L. ferruginosa atricapilla*) = *Lonchura*.
- Donacola* Gould, 1842. (*L. castaneothorax*) = *Lonchura*.
- Emblema* Gould, 1842. (*Z. pictus*) = *Zonaeginthus*.<sup>6</sup>
- Erythrura* Blyth, 1852. (*E. prasina*) = *Erythrura*.
- Erythrura** Swainson, 1837. (*E. prasina*).
- Estrilda** Swainson, 1827. (*E. astrild*).
- EUODICE** Reichenbach, 1862. (*L. cantans*). Subgenus of *Lonchura*.
- Glaucestrilda* A. Roberts, 1922. (*E. coerulescens*) = *Estrilda*.
- Gouldaeornis* Mathews, 1923. (*P. gouldiae*) = *Poephila*.
- Granatina* Bonaparte, 1850. (*E. granatina*) = *Estrilda*.
- Habropyga* Cabanis, 1827. (*E. astrild*) = *Estrilda*.
- Haplopyga* Heuglin, 1873. (*E. astrild*) = *Estrilda*.
- ETEROMUNIA** Mathews, 1913. (*L. pectoralis*). Subgenus of *Lonchura*.
- Hypargos** Reichenbach, 1862. (*H. margaritatus*).
- LAGONOSTICTA** Cabanis, 1851. (*E. rubricata*). Subgenus of *Estrilda*.
- Lepidopyga* Reichenbach, 1862. (*L. nana*) = *Lonchura*.
- Lichnospiza* Heuglin, 1871. (*E. rara*) = *Estrilda*.
- Lobospiza* Hartlaub and Finsch, 1870. (*E. notabilis* = *cyanovirens*) = *Erythrura*.
- Lobospingus* De Vis, 1897. (*E. trichroa sigillifera*) = *Erythrura*.
- Lonchura** Sykes, 1832. (*L. punctulata*).
- Maja* Bonaparte, 1850. (*L. maja*) = *Lonchura*.
- MANDINGOA** Hartert, 1919. (*H. nitidulus*). Subgenus of *Hypargos*.
- Mariposa* Reichenbach, 1863. (*E. angolensis bengala*) = *Estrilda*.
- Marquetia* Reichenbach, 1863. (*P. melba*) = *Pytilia*.
- Melpoda* Reichenbach, 1863. (*E. melpoda*) = *Estrilda*.
- Mormolycea* Reichenbach, 1863. (*E. larvata*) = *Estrilda*.
- MUNIA** Hodgson, 1836. (*L. ferruginosa atricapilla*). Subgenus of *Lonchura*.
- Neisna* Bonaparte, 1850. (*E. subflava*) = *Estrilda*.
- NEOCHMIA** Gray, 1849. (*P. phaeton*). Subgenus of *Poephila*.
- Neopoephila* Mathews, 1913. (*P. personata*) = *Poephila*.
- Nesocharis* Alexander, 1903. (*E. shelleyi*) = *Estrilda*.
- Nigrita** Strickland, 1841. (*N. canicapilla*).
- Odontospiza* Oberholser, 1905. (*L. griseicapilla*) = *Lonchura*.
- Oreospiza* De Vis, 1897. (*Z. fuliginosus*) = *Zonaeginthus*.
- OREOSTRUTHUS** De Vis, 1898. (*Z. fuliginosus*). Subgenus of *Zonaeginthus*.
- ORTYGOSPIZA** Sundevall, 1850. (*E. atricollis polyzona*). Subgenus of *Estrilda*.
- Oryzornis* Cabanis, 1851. (*P. oryzivora*) = *Padda*.
- Oxyerca* Gray, 1842. (*L. punctulata*) = *Lonchura*.
- Padda** Reichenbach, 1850. (*P. oryzivora*).
- Paludipasser* Neave, 1909. (*E. locustella*) = *Estrilda*.
- Parmoptila** Cassin, 1859. (*P. woodhousei*).
- Pernopsis* Heine, 1860. (*N. fusconota*) = *Nigrita*.
- Pirenestes** Swainson, 1837. (*P. sanguineus*).
- Poephila** Gould, 1842. (*P. acuticauda*).
- Pytilia** Swainson, 1837. (*P. phoenicoptera*).
- RAMPHOSTRUTHUS** Mayr, 1931. (*E. kleinschmidti*). Subgenus of *Erythrura*.
- REICHENOWIA** Poche, 1904. (*E. hyperhythra*). Subgenus of *Erythrura*.
- Rhodopyga* Heuglin, 1868. (*E. senegala brunneiceps*) = *Estrilda*.
- Spermestes* Swainson, 1837. (*L. cucullata*) = *Lonchura*.
- Spermophaga** Swainson, 1837. (*S. haematina*).
- Spermospiza* Gray, 1840. (*S. haematina*) = *Spermophaga*.
- Sporaeginthus* Cabanis, 1850. (*E. subflava*) = *Estrilda*.
- Sporathastes* Cabanis, 1847. (*A. fasciata*) = *Amadina*.
- Steganopleura* Bonaparte, 1850. (*P. biichenovi*) = *Poephila*.

<sup>6</sup> *Emblema* Gould, 1842, is invalidated by *Amblema* Rafinesque altered to *Emblema* by Deshayes, 1840 (Dict. d' H. N., vol. 1, p. 334).

- Stictoptera* Reichenbach, 1862. (*P. bichenovi*) = *Poephila*.
- Stictospiza* Sharpe, 1890. (*E. formosa*) = *Estrilda*.
- Stizoptera* Oberholser, 1899. (*P. bichenovi*) = *Poephila*.
- Taeniopygia* Reichenbach, 1862. (*P. guttata castanotis*) = *Poephila*.
- Tavistocka* Mathews, 1919. (*Z. guttatus*) = *Zonaeginthus*.
- Trichogramaptila* Reichenbach, 1862. (*L. striata*) = *Lonchura*.
- Trichroa* Reichenbach, 1862. (*E. trichroa*) = *Erythrura*.
- Uraeginthus* Cabanis, 1851. (*E. angolensis bengala*) = *Estrilda*.
- Uroloncha* Cabanis, 1851. (*L. punctulata*) = *Lonchura*.
- Zonaeginthus** Cabanis, 1851. (*Z. bellus*).
- Zonogastris* Cabanis, 1851. (*P. phoenicoptera*) = *Pytilia*.



## 12.

## The Relationship Between Weight and Body Form in Various Species of Scombroid Fishes.

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(Text-figures 1-12).

Organic growth may be defined as increase of the whole organism or any of its systems in weight or in the size of any of its component parts. As thus interpreted growth can be distinguished from differentiation, which represents increase in organization as apart from any measurable increase in the size or weight of an organic system. Growth broken down into its multitude of single processes is difficult to interpret quantitatively, but the direction and amount of growth, considered as a mere quantitative increase of the whole or of its component parts (each of which is the result of a multitude of processes) may be subjected to mathematical analysis. The use of formulas will thus indicate the nature and the types of changes occurring during the life of the organism, although it does not provide an interpretation of the causes of growth.

It has been found that organisms generally show a positive acceleration of growth during early development, after which the velocity shows a negative acceleration. In many investigations the available data cannot take into consideration this time factor, but other growth phenomena may nevertheless be analyzed. Thus the analysis of relative growth indicates how added increments, no matter how small, are being distributed to the component parts of the organism. Relative growth, as distinct from simple growth analysis, does not deal alone with the increase in general size, but rather with the growth and size of any dimension in relation to that of another dimension. These relations determine the form of the organism.

In this paper relative growth methods are used to determine the relation between weight and body form in several fishes generally classed in the suborder Scombroidei. The changes in form during growth are indi-

cated by the analysis of the relative measurements of length, depth and width, as correlated with changes in weight. The mathematical analyses of relative growth during ontogeny exhibit what appear to be fundamental trends and similarities in the type of growth of related species. These developmental likenesses suggest the possible use of such analyses in determining phylogenetic relationships.

## METHOD OF ANALYSIS.

The equation  $y = bx^k$  has been used by various workers to express the growth of a part ( $y$ ) relative to that of another part or the remainder of the body ( $x$ ). The exponent  $k$  denotes the constant differential rate of increase of the variables, whereas  $b$ , in its simplest connotation, expresses the value of  $y$  when  $x$  is equal to one. When applied in logarithmic form the equation becomes  $\log y = k \log x + \log b$ , and the resulting curve is a straight line the value of which is determined by its slope. That a straight line will fit a considerable range of data on differential growth is well substantiated. For example this relation holds for the growth of the large chela of the male fiddler crab, *Uca pugnax*, relative to that of the remainder of the body (Huxley, 1932); for the growth of the jaws of certain fishes, *Lepisosteus osseus*, *Belone* and *Hemirhamphus far*, relative to that of the remainder of the body (Needham, 1935); and that of the abdomen of the pea-crab, *Pinnothereus pisum*, relative to that of the carapace (Williams and Needham, 1938).

This empirical equation adequately states the ontogenetic change in the relative size of the parts or organs under consideration, despite the fact that the exponential value  $k$  lacks dimensions and is a "pure number." Growth is basically dependent on the multiplication of living substance, but the increase in each part of the organism occurs at a specific rate. As growth progresses there

<sup>1</sup> The field work and writing of the paper were supported by the Ichthyological Research Fund of the Museum. This paper is Number 25 in the Lerner Ichthyological Series.

occur various readjustments and changes in proportions, depending on the relative growth rates. These changes can be readily analyzed by the logarithmic method.

The use of the equation  $y = bx^k$  has been extended for a study of other relationships. A specific instance, where weight ( $y$ ) has been assumed to be proportionate to the cube of the length ( $k=3$ ), has been employed by Crozier and Hecht (1913), Hecht (1916), and Van Oosten (1928) to study the relationship of weight to length in fishes. Keys (1928) and Marshall, Nicholls and Orr (1937) have also studied this relationship of weight to length and have demonstrated the applicability of the equation when both  $b$  and  $k$  are determined empirically.

The use of different terms by various workers has confused the literature on relative growth. Since the equation expresses the growth of a part relative to the whole or another part,  $k$  was first termed the constant differential growth ratio (Huxley, 1924). In a revision of terminology, Huxley and Tessier (1936) preferred to designate  $k$  as the equilibrium constant. The value of  $b$ , the size of the organ or part when the standard is 1, has been referred to as the initial growth index. It is a theoretical number, representing the intercept value of the regression line, and does not actually indicate the weight, depth or width of the fish having a length of 1, but it does define the proportionate relations of the fish, beginning at the length at which the straight line relations for relative growth are established. The growth ratio ( $k$ ) indicates the relative sizes of the increments of each variable during growth and is thus indicative of the proportional changes in the dimensions. When one part grows at the same rate as another part of the body ( $k=1$ ), the relative increases in growth of the two variables are equal and the proportions remain undisturbed. Pezard (1918) denotes this specific condition of growth "isogonic" and this term was adopted by early workers. Other terminology used to designate such growth has been "harmonic growth" (Champy, 1929) and "isometry" (Huxley and Tessier, 1936). If the rates are unequal, growth is said to be heterogonic (disharmonic, or allometric) in a positive or negative direction. When the dependent variable ( $y$ ) increases at a rate greater than that of the part or organ ( $x$ ) to which it is being compared, the allometry is positive. If the constant differential growth ratio is less than unity the relationship is such that the dependent variable shows negative allometry.

A number of difficulties have been pointed out by various workers in the use of the logarithmic representation. Gray (1929) explains the obvious effect upon apparent variation that logarithmic representation necessarily introduces. With the transformation

to logarithmic values the diameter of a dot on the graph may be greater than the error of the measurement of the variable, since the scale of the graph becomes proportionally smaller with the larger measurements. Thus when the dots are extremely close together they may fit the line of the curve and yet conceal small but significant variations. For this reason, in a study of allometric growth, statistical methods, rather than graphical procedures, should be used for the determination of the constants.

Another difficulty arises in the grouping of the data. The use of averages will minimize the natural variation of the larger specimens and overemphasize that of the smaller specimens. Therefore in grouping the data for this study the actual data were first converted to their logarithmic values and then grouped according to the increasing geometric scale. In this manner the variation for the larger specimens was given the same value as that for the smaller specimens.

The value of the growth constants was determined by the use of the product moment method. In the analysis of such data most workers have made use of only one regression line—that of the dependent variable in relation to the independent variable. Statistically this equation is known as the regression of  $y$  upon  $x$ . Because of the irregularities in variation shown by anything less than an infinite number of specimens, a single regression line will not fit a series of data, especially those collected under different environmental conditions. Therefore another regression line of the best value for the independent variable in relation to the dependent variable (the regression of  $x$  upon  $y$ ) has been determined. The regression value for  $x$  upon  $y$  has been converted to its reciprocal value so as to be expressed in the same terms as the regression of  $y$  upon  $x$ . Two such regression lines make interpretation difficult but the mean regression line, determined from the two, will give a simple average value for all the available data. These mean regression lines are conveniently comparable. Each such line contains a theoretical  $k$  value and since the two  $k$  values for each regression are very similar (compare  $k_{yx}$  and  $k_{xy}$  in Tables 2, 3), the value of  $k$  for the mean regression line  $k_{av}$  must be near its true value.

#### METHOD OF WEIGHING AND MEASURING.

Because of considerable postmortem changes, measurements and weights were taken as soon as possible after the fish were out of the water. Tests made of weight changes due to water loss or gain during the brief intervening period showed negligible differences. Some of the fish were kept alive until weighed and measured. Weight for the smallest fish was determined

TABLE 1. VALUES OF  $n$  AND  $a$  FOR THE PARTITION OF GROWTH INCREMENTS OF BODY WEIGHT RELATIVE TO THE STANDARD BODY LENGTH.

The exponent  $n_{yz}$  gives the values for the regression line of weight upon length;  $n_{xy}$  is the value for length increase upon weight, but still expressed in terms of the standard length, and  $n$  is the geometric mean value for  $n_{yz}$  and  $n_{xy}$ . The species for the various families are arranged in descending order for the value of  $a$ . The range of the data for the weight in grams and the length in millimeters is given for each species.

SPECIES	$n_{yz}$	$n_{xy}^*$	$n$	$a$	RANGE	
					WEIGHT IN GRAMS	LENGTH IN MM.
Pomatomidae						
<i>Pomatomus saltatrix</i>	2.962	3.001	2.98	.0000229	65.0 — 1040	145— 363
Carangidae						
<i>Caranx hippos</i>	2.779	2.829	2.80	.0000858	51.0 — 738	116— 312
<i>Vomer setapinnis</i>	2.823	2.849	2.84	.0000648	5.4 — 158	55— 180
<i>Caranx crysos</i>	2.838	2.892	2.87	.0000562	22.6 — 201	96— 203
<i>Selene vomer</i>	2.957	2.989	2.97	.0000483	1.3 — 79	30— 122
<i>Trachinotus falcatus</i>	3.082	3.107	3.09	.0000350	.06— 3	11— 39
<i>Trachinotus carolinus</i>	3.044	3.054	3.05	.0000264	.07— 773	14— 304
Scombridae						
<i>Scomberomorus maculatus</i>	2.825	2.849	2.84	.0000288	57.0 — 1730	167— 552
Trichiuridae						
<i>Trichiurus lepturus</i>	3.352	3.374	3.36	.0000000674	8.8 — 396	263— 810
Istiophoridae						
<i>Makaira nigricans ampla</i>	3.313	3.679	3.49	.000000161	41220.0 — 243260	1950—3040
<i>Makaira nigricans marlina</i>	3.500	3.582	3.54	.000000118	47560.0 — 369200	1950—3290

\* The values given in this column are the reciprocal values of  $n_{xy}$ . They express the increase of length upon weight in terms of the standard length.

by a chemical balance, for the medium-sized ones by a triple balance scale, and for the largest by a spring scale. Standard length is here expressed as the distance from the tip of the snout to the vertical of the minimum depth of the caudal peduncle (that is, to approximately opposite the front edge of the hypural plate). For each species the depth was taken at the same point on each specimen, yielding the maximum measurement; correction was made to compensate for distension due to stomach contents. Width was taken where greatest.

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THE LENGTH-WEIGHT RELATIONSHIP.

Early work on the relationship of weight to length resulted in the formulation of the cube law by Spencer (1871). Hecht (1916), Van Oosten (1928) and others further applied this principle to the growth of fishes. Most of these authors assumed that there exists, in fish, a long-continued period with no change in external proportions (or in specific gravity) and consequently that, in the equation  $y=bx^k$ ,  $k$  is equal to 3. These workers were thus necessarily concerned only with the variation of the coefficient  $b$ . If the cube law holds for the greater portion of the fish's life, it would necessarily mean that the final form is established early and that enlargement in each dimension is a linear function of length. Secondly the density must remain unchanged in order to avoid allometric growth.

There are theoretical limitations to the simple cubic function, since the direct relationship is between length and volume, rather than between length and mass. Mass is proportional to volume only in a body of constant density. Hence in expressing the weight of a complex heterogeneous body in

TABLE 2. VALUES OF  $k$  AND  $b$  FOR THE PARTITION OF INCREMENTS OF BODY DEPTH RELATIVE TO THE STANDARD BODY LENGTH.

The exponent  $k_{yx}$  denotes the value for the regression line of depth upon length;  $k_{xy}$  is the value for length increase upon depth, but still expressed in terms of the standard length, and  $k$  is the geometric mean value for  $k_{yx}$  and  $k_{xy}$ . The species of the various families are arranged in descending order for the value of  $b$ . The range of the data for depth and length, both in millimeters, is given for each species.

SPECIES	$k_{yx}$	$k_{xy}^*$	$k$	$b$	RANGE IN SIZE	
					DEPTH	LENGTH
Pomatomidae						
<i>Pomatomus saltatrix</i>	0.865	0.903	0.88	0.529	41.0—102	145— 363
Carangidae						
<i>Vomer setapinnis</i>	0.744	0.764	0.75	1.970	39.0—110	55— 180
<i>Selene vomer</i>	0.914	0.925	0.92	1.140	28.0— 94	30— 122
<i>Caranx hippos</i>	0.794	0.821	0.81	1.060	49.0—102	116— 312
<i>Caranx crysos</i>	0.870	0.927	0.90	0.581	34.0— 66	96— 203
<i>Trachinotus falcatus</i>	1.235	1.257	1.25	0.259	5.4— 25	11— 39
<i>Trachinotus carolinus</i>	1.127	1.131	1.13	0.251	4.6—124	14— 304
Scombridae						
<i>Scomberomorus maculatus</i>	0.860	0.884	0.87	0.414	40.0—109	167— 552
Trichiuridae						
<i>Trichiurus lepturus</i>	1.166	1.187	1.18	0.022	15.3— 57	263— 810
Istiophoridae						
<i>Makaira nigricans marlina</i>	1.175	1.298	1.24	0.033	384.0—760	1950—3290
<i>Makaira nigricans ampla</i>	1.213	1.433	1.32	0.016	330.0—670	1950—3040

\* These values are the reciprocals of the regression values for increase of length ( $x$ ) upon weight ( $y$ ). They express the increase of  $x$  on  $y$  in terms of the standard length.

terms of length the equation would hardly be expected to take the form of a cubic parabola although it may approximate one. The specific gravity of the watery environment of most fishes remains fairly constant, and as free-swimming fishes like the Scombroidei are in close hydrostatic equilibrium with their environment they must maintain a constant specific gravity. If there are uncompensated changes in the specific gravity of the fish (due to the altered density of various parts of the organism, such as bone or adipose tissue, or altered proportions of these parts), and if the specific gravity remains in equilibrium with the surroundings, some change in body form would be necessitated. Therefore changes in the dimensions of the body may compensate for a tendency toward change in density and thus maintain the organism at a specific gravity equal to that of the surrounding medium.

It is now commonly recognized, as the result of numerous researches, that the cube relationship between weight and length is only an approximation, and at times is not even closely realized. The application of the allometric formula,  $y = bx^k$ , for a study of the relationship of weight to length has been applied successfully by various workers to the post-metamorphic period of fish development. Keys (1928) demonstrated that the weight of the killifish (*Fundulus parvipinnis*), the European herring (*Clupea haren-*

*gus*), and the California sardine increases at a rate greater than the cube of the length and less than the fourth power of the length. In an analysis of the growth of the blue marlin, Shapiro (1938) demonstrated greater increments of weight relative to increasing increments of length ( $k > 3.00$ ) and that form change was taking place during the post-metamorphic growth. By means of statistical methods Keys was able to show that variations in both  $k$  and  $b$  denote change of form. Therefore, if we are to study adequately the implications of weight in relation to form the equation should be determined empirically.

The formula  $W = aL^n$  implies the same conditions that have been expressed for the growth of a part relative to another part or the remainder of the body. Weight ( $W$ ) and length ( $L$ ) are the variables under consideration; the exponent  $n$  indicates the relative increases of these variables during the growth of the fish. The coefficient  $a$  is indicative of the units of measurement used (Keys, 1928) and also denotes the value of the weight when the length is mathematically equal to 1. It thus serves as an index of the initial relationship existing between the two variables at the point where both are reduced to a single theoretical unit. It is true that  $a$  will fluctuate seasonally with-

<sup>2</sup> These symbols are used for the allometry formula of weight in relation to length as distinguishable from the general formula,  $y = bx^k$ , to denote relationships of dimensions, i.e., width and depth.

TABLE 3. VALUES OF  $k$  AND  $b$  FOR THE PARTITION OF INCREMENTS OF BODY WIDTH RELATIVE TO THE STANDARD BODY LENGTH.

The exponent  $k_{yx}$  denotes the value for the regression line of width upon length,  $k_{xy}$  is the value for length increase upon width, but still expressed in terms of the standard length, and  $k$  is the geometric mean value for  $k_{yx}$  and  $k_{xy}$ . The species are arranged in descending order, within each family, for the value of  $b$ . The range of data for width and length, both in millimeters, is given for each species.

SPECIES	$k_{yx}$	$k_{xy}$ *	$k$	$b$	RANGE IN SIZE	
					DEPTH	LENGTH
Pomatomidae						
<i>Pomatomus saltatrix</i>	1.170	1.236	1.20	0.040	16.0— 49	145— 363
Carangidae						
<i>Caranx crysos</i>	1.014	1.107	1.06	0.109	13.0— 57	96— 203
<i>Caranx hippos</i>	1.091	1.145	1.12	0.086	18.0— 49	116— 312
<i>Selene vomer</i>	1.065	1.079	1.07	0.086	4.1— 15	30— 122
<i>Vomer setapinnis</i>	1.107	1.131	1.12	0.057	5.3— 20	55— 180
<i>Trachinotus carolinus</i>	1.034	1.042	1.04	0.012	3.1— 40	22— 304
Scombridae						
<i>Scomberomorus maculatus</i>	1.075	1.114	1.10	0.057	16.0— 55	167— 552
Trichiuridae						
<i>Trichiurus lepturus</i>	1.318	1.344	1.33	0.0025	4.2— 19	263— 810
Istiophoridae						
<i>Makaira nigricans marlina</i>	1.313	1.533	1.42	0.0040	190.0—425	1950—3290
<i>Makaira nigricans ampla</i>	1.230	1.725	1.46	0.0027	165.0—320	1950—3040

\* These values are the reciprocals of the regression values for increase of length ( $x$ ) upon width ( $y$ ). They express the increase of  $x$  on  $y$  in terms of the standard length.

in the limits of variation and consequently some investigators (mostly those who have worked with the cube law) have used this coefficient as a measure of the condition of the fish or the state of sexual development. We prefer to use it not as a measure of fluctuating heaviness but of relative bulk, specific for each type of fish.

The empirical determination of the relationship between weight and length shows that each species maintains its specific growth ratio. The range of the exponent  $n$  is from 2.80 in *Caranx hippos* to 3.54 in *Marlina nigricans ampla* (Table 1, Text-figs. 1-4)<sup>3</sup>. Those species with a value below 3.00 are maintaining a negatively allometric increase of weight for each unit increase of the length. Thus, among the carangids, *Caranx hippos* and *C. crysos* (Text-fig. 1) and *Selene vomer*<sup>4</sup> and *Vomer setapinnis* (Text-fig. 2) become relatively lighter with increase in length. Among the species studied of closely allied families, *Scomberomorus maculatus* shows a similar condition.

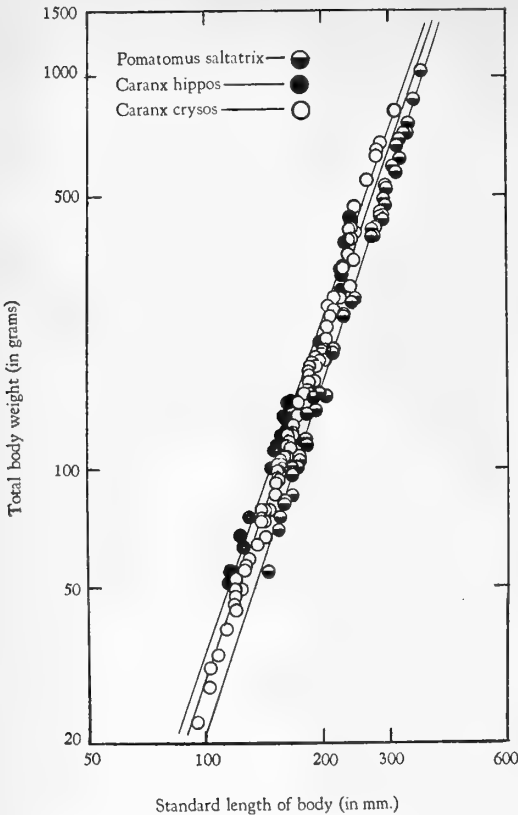
The weight increases exactly as the cube of the length only when an isometric relation between these variables is maintained. This is a special case of growth similar to

the previously-explained isometric condition, where linear dimensions were considered, but here growth would proceed either isometrically along all three geometric axes, or the allometric growth along different axes would be exactly compensating. The only species approximately showing this special isometric length-weight relation is the bluefish (*Pomatomus saltatrix*). For this species the value of  $n$  is 2.98 but the regression of weight on length shows a value of 2.962 and of length on weight 3.001 (Table 1). If we interpret this almost ideal weight-cube-length relationship on the basis of no change in form (as the cube law would demand), *P. saltatrix* should maintain constancy of body form during growth. The linear dimensions of depth and width, however, show no approach to the condition of unchanging proportions. The constant differential partition of growth increments in relation to the length is 0.88 for the depth (Table 2) and 1.20 for the width (Table 3). Since these exponential values deviate about equally from the value (1.00) for isometric growth they are approximately compensating, and the weight increases about as the cubic function of the length.

The remaining species studied show a positive allometric increase of weight in terms of length. *Trachinotus carolinus* and *T. falcatus* show a slight tendency to become heavier with increase in length (Text-fig. 3, Table 1) but *Trichiurus lepturus* and

<sup>3</sup> The growth constants for *Caranx crysos* have been determined only for those fish up to 203 mm. in standard length. The specimens above this size depart significantly from the curve in a more positive direction. Whether this deviation is due to a change in the growth rate at this point or to an insufficiency of accurate measurements cannot be determined as yet.

<sup>4</sup> *Selene vomer* is currently recognized as being synonymous with *Argyreus vomer*.



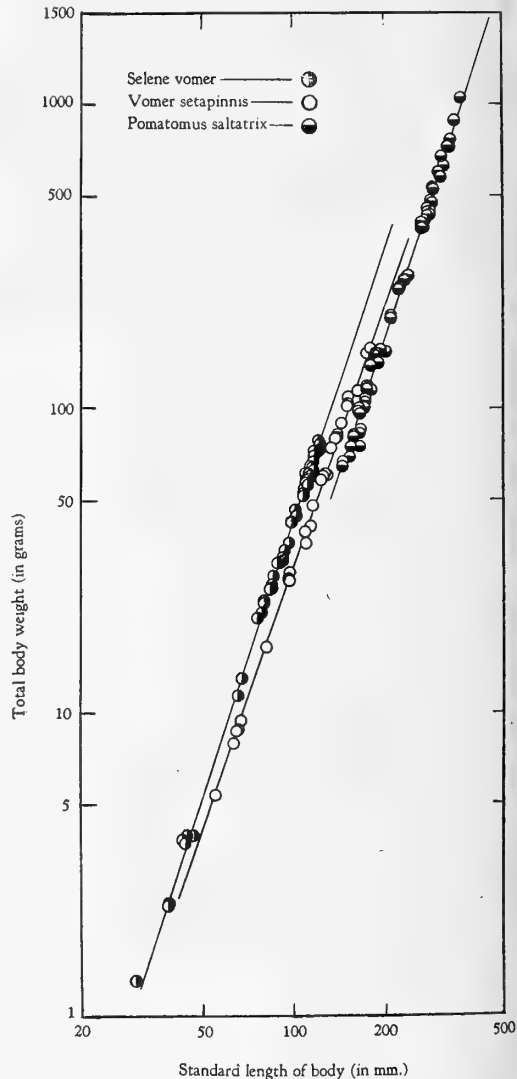
TEXT-FIG. 1. Increase of total body weight with standard body length; logarithmic plotting for both weight and length.

both subspecies of *Makaira* maintain a high positive allometry (Text-fig. 4, Table 1).

In studies of length-weight relations the measurement of maximum length, depth and width have been uncritically accepted as representing precisely the form of the fish throughout life. Changes in shape, however, may take place in portions of the body which have not been measured, for instance the head and peduncular regions. In an analysis of numerous dimensions of *Makaira nigricans ampla* (Shapiro, 1938), the gradients for different parts of the fish were shown to differ considerably, the tendency being for the exponential values to be more intense posteriorly and less so anteriorly. Only if the shape of all sagittal and all frontal sections remained constant, would the maximum depth and width measurements accurately represent the form. In that case the sum of the exponential values for the three axes should equal the value of  $n$  in the length-weight formula. *Selene vomer* and *Vomer setapinnis* are the only species in this study that maintain such a condition (Table 4), although the possibility still exists that various sections of their body too

may be growing at different rates, since positive exponential values in some sections of the body may just compensate negative values in other parts. The results obtained with the remaining species indicate that unmeasured proportions of the body change with age, for the sum of the exponents of the linear dimensions often does not closely approximate the value of  $n$  (Table 4).

A comparison of the initial growth index ( $a$ ) with the size attained by the various species indicates that the larger fish tend to show a smaller coefficient of bulkiness (Table 1). At the inception of the post-metamorphic straight line relation *Trichiurus lepturus* ( $a=0.0000000674$ ) and *Makaira nigricans ampla* ( $a=0.000000161$ ) and



TEXT-FIG. 2. Total body weight against standard length; logarithmic plotting both ways.

TABLE 4. SUM OF EXPONENTS FOR LINEAR DIMENSIONS COMPARED WITH EXPONENT FOR LENGTH-WEIGHT RELATIONSHIP.

If the three geometric axes of length, depth and width adequately represent the form of the body, the sum of their exponential values should equal the value of  $n$  for the length-weight relation. If the sum of the  $k$  values of these axes does not closely approximate the value of  $n$ , changes in shape of other portions of the body are taking place and the maximum measurements of length, depth and width are not truly representative of the form of the body.

	VALUE OF $k$ FOR			SUM, 1+2+3	VALUE OF $n$
	(1) LENGTH	(2) DEPTH	(3) WIDTH		
<i>Pomatomus saltatrix</i>	1.00	0.88	1.20	3.08	2.98
<i>Caranx hippos</i>	1.00	0.81	1.12	2.93	2.80
<i>Caranx crysos</i>	1.00	0.90	1.06	2.96	2.87
<i>Vomer setapinnis</i>	1.00	0.75	1.12	2.87	2.84
<i>Selene vomer</i>	1.00	0.92	1.07	2.99	2.97
<i>Trachinotus carolinus</i>	1.00	1.13	1.04	3.17	3.05
<i>Scomberomorus maculatus</i>	1.00	0.87	1.10	2.97	2.84
<i>Trichiurus lepturus</i>	1.00	1.18	1.33	3.51	3.36
<i>Makaira nigricans ampla</i>	1.00	1.32	1.46	3.78	3.49
<i>Makaira nigricans marlina</i>	1.00	1.24	1.42	3.66	3.54

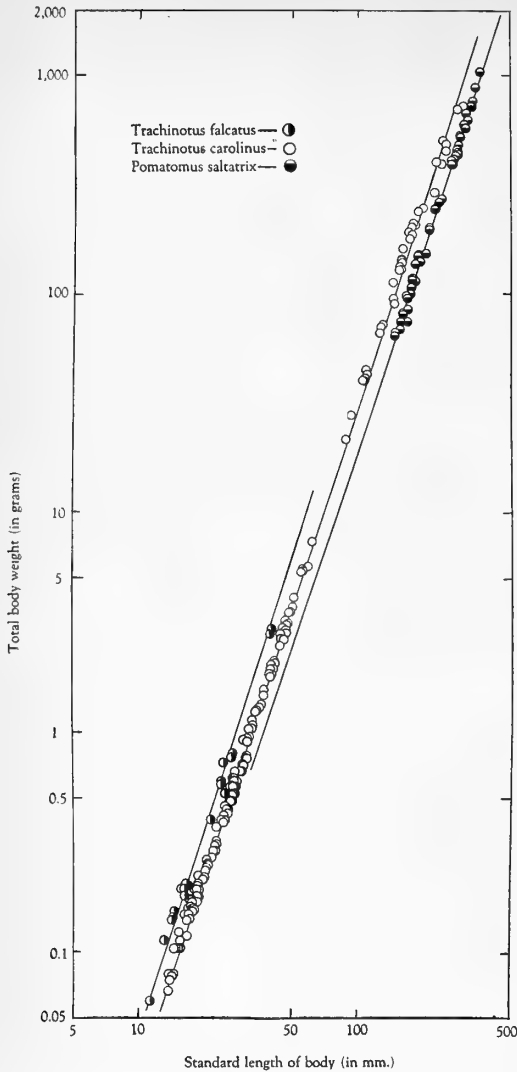
*M. n. marlina* ( $a=0.000000118$ ) have decidedly smaller bulk per unit length than do the deeper-bodied and shorter forms of the carangids, such as *Vomer setapinnis* ( $a=0.0000648$ ) and *Selene vomer* ( $a=0.0000483$ ). In its  $a$  value of 0.0000288, *Scomberomorus maculatus* approaches slightly the condition of the specialized fusiform Istiophoridae and the elongate Trichiuridae. The value of  $a$  for *Trachinotus carolinus* (0.0000264) and *T. falcatus* (0.0000350) is low as compared with the other carangids. It is similar to the value for a central scombrid form like *S. maculatus*. Thus, for unit length, the longer fish, at the point where differentiation has been completed and post-metamorphic growth is beginning to follow the straight line relation, show a low weight coefficient as compared with the high value for the deep-bodied forms.

If  $a$  is accepted as an indicator of the type of body form, the eleven species of fish can be arranged in a series grading from the deep-bodied to the elongate type. The use of the initial growth index for this purpose disregards the changes in body form that take place during post-metamorphic growth. The value of  $a$  is high for the deep-bodied compressed forms such as *Selene vomer* and *Vomer setapinnis*. Their greater relative bulkiness at the beginning of the post-metamorphic growth period seems to be directly correlated with their extreme depth and shortness of body. The moderately elongated fusiform type, represented by the mackerel, bluefish and pompano (*Trachinotus carolinus*), show central values of  $a$  (smaller bulkiness per unit length than in the deep-bodied forms). The most specialized, elongated types, represented by the cutlass fish (*Trichiurus lepturus*), give the low values at the other extreme of the series. In this species the theoretical bulk

per unit length at the beginning of the post-metamorphic period is incredibly small. It should be pointed out that the standard length of the marlins was determined with the enormous bill included. The value of  $a$  would be somewhat higher if the sword were discounted and would place them closer to the category of the fusiform mackerel type.

That there is a relationship between  $a$  and  $n$  can be shown by plotting these values for the different species on semi-log paper (Text-fig. 5). The general tendency is such that  $n$  increases in arithmetical progression as  $a$  decreases in geometrical progression, thus conforming to an exponential function wherein  $\log a$  shows a definite rate of decrease in terms of increase of  $n$ . Hersh (1931, 1934) found that, in the relative growth of genetic mutants of *Drosophila* and in the evolutionary relative growth of the Titanotheres, this same exponential relationship holds true. Lumer (1939) also obtained an inverse relationship between the constants for the radius-humerus and leg-arm relations in the Pongidae. Thus, if the value for  $a$  suggests a slim fish per unit length at the termination of its larval growth, its weight increase, relative to the length, for the post-metamorphic period is correspondingly greater (compare values for  $a$  and  $n$  in Table 1). *Makaira nigricans ampla*, *M. n. marlina* and *Trichiurus lepturus*, with the low  $a$  values of a slim fish, show a steeper gradient for the distribution of weight as the fish increases in length, whereas the reverse is true of the deeper-bodied fish. The trend of  $a$  in relation to  $n$  for the various families has been indicated by the broken lines on Text-fig. 5. It may signify that the exponential relationship is distinctive for each family and therefore of some value in determining phylogenetic trends.

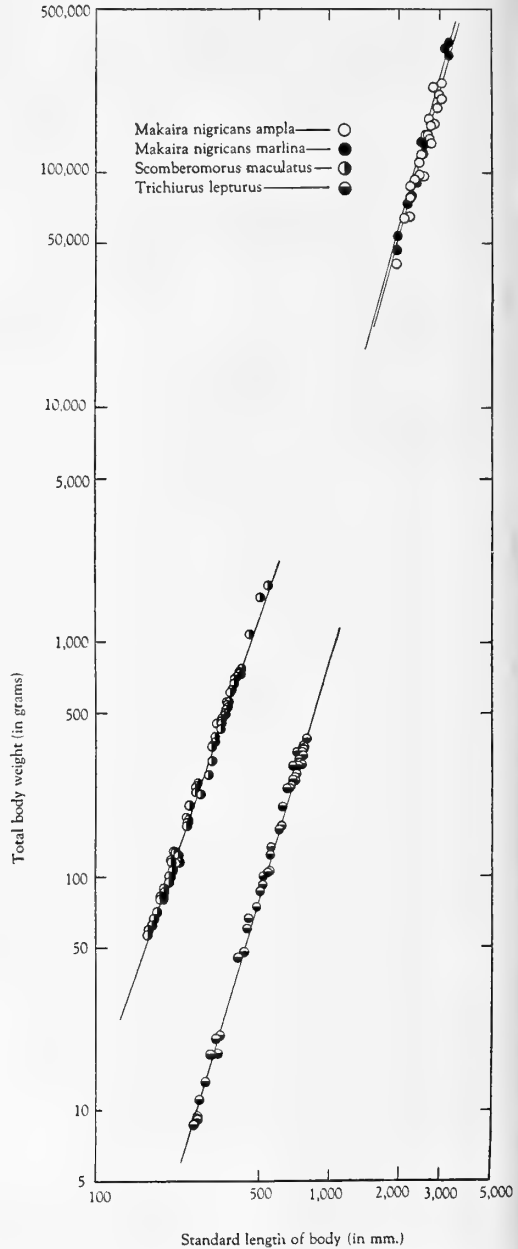




TEXT-FIG. 3. Increase of body weight with increase of standard body length; logarithmic plotting both ways.

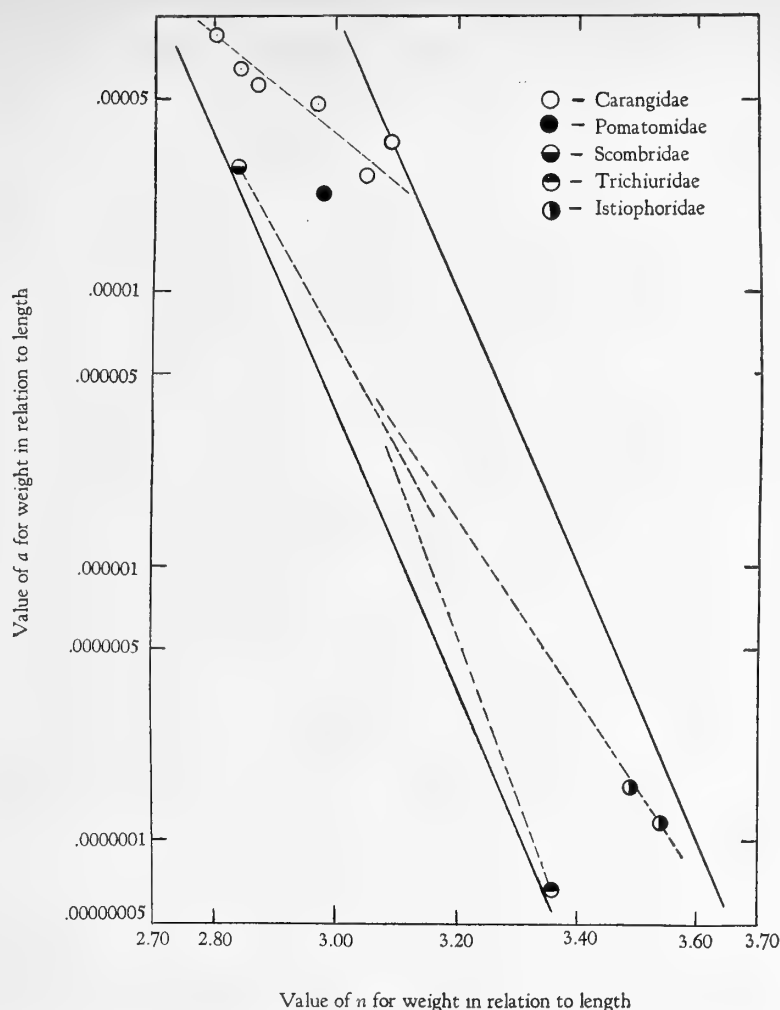
The values of  $n$  (Table 1) indicate that closely allied members of the various families tend to have similar coefficients of growth partition. The species *Caranx hippos* and *C. crysos* have values of 2.80 and 2.87 respectively, *Trachinotus carolinus* 3.05 and *T. falcatus* 3.09, and *Makaira nigricans ampla* 3.49 and *M. n. marlina* 3.54. Although similar within each genus, the species of *Caranx* and of *Trachinotus* show no overlapping of the regression lines for  $n_{yx}$  and  $n_{xy}$  (Table 1). Therefore the species can be separated by their constant differential growth ratio, as well as by differences in weight at the same length. *T. falcatus* is relatively heavier than *T. carolinus* and *C.*

*hippos* relatively heavier than *C. crysos* (refer to Text-figs. 1 and 3). There is a distinct tendency for convergence between the species of *Caranx* (eventually the index of weight to length becomes the same for both), but for divergence between the species of *Trachinotus*. The relative growth rates for the post-metamorphic period appear to be broadly similar for closely re-



TEXT-FIG. 4. Total body weight relative to standard body length; logarithmic plotting both ways.





TEXT-FIG. 5. Values of  $a$  for weight in relation to length plotted logarithmically against the growth coefficients ( $n$ ) for weight relative to length;  $n$  plotted on an arithmetic scale.

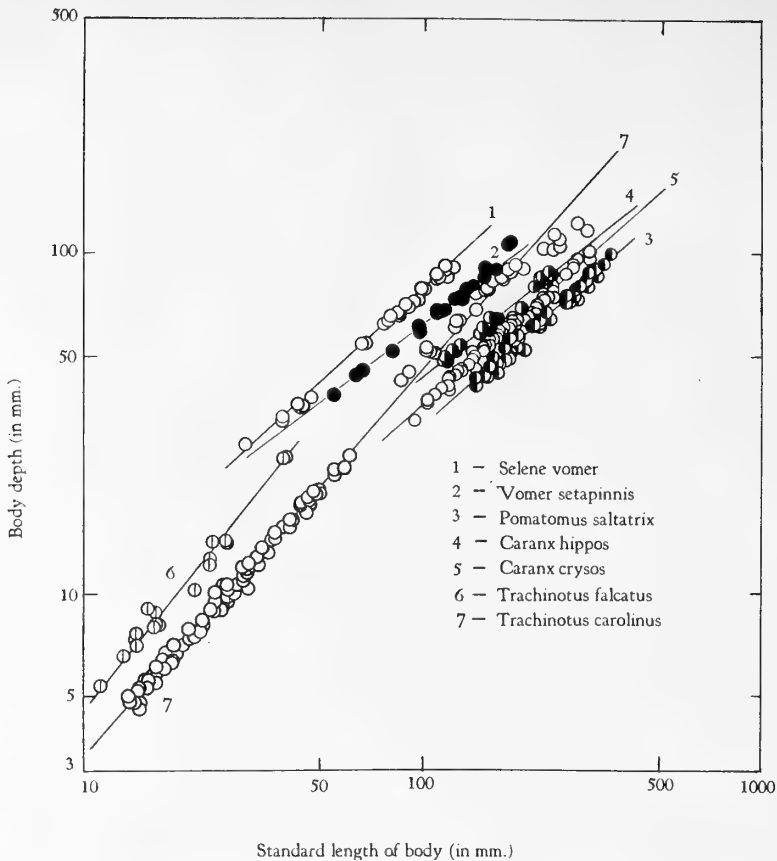
lated species, but specific differences are maintained.

#### DEPTH AND WIDTH AS A MEASURE OF BODY FORM.

For the body measurements (depth and width in relation to length) the relationships are linear and have been expressed either by the equation  $y = a + bx$  or by the geometric form  $y = bx^k$ . Which equation is more applicable to the data? Meek (1905) and Hecht (1916) used the first equation, for they maintained that, if the lines for the growth of the dimensions of the body converge to zero when plotted in relation to the length, the equation becomes  $y = bx$ . This isometry equation is therefore applicable when the growth coefficient is close to 1

and will fit the data as well as the allometry formula. But what of the instances when the data does not show the specific case of isometry? The first equation ignores the difference of  $k$  from one, whereas the second equation ignores the difference of  $a$  from zero. If the growth involved is geometric the factor  $a$  is small and no valid error results from ignoring it. Simpson and Roe (1939, p. 370) show that the allometry formula fits the facts better than does the isometry formula when growth is markedly allometric, as it often is.

The values for the constant differential partition of depth in relation to length show negative allometry for some species, and definitely positive allometry for others. Among the Carangidae the values for the



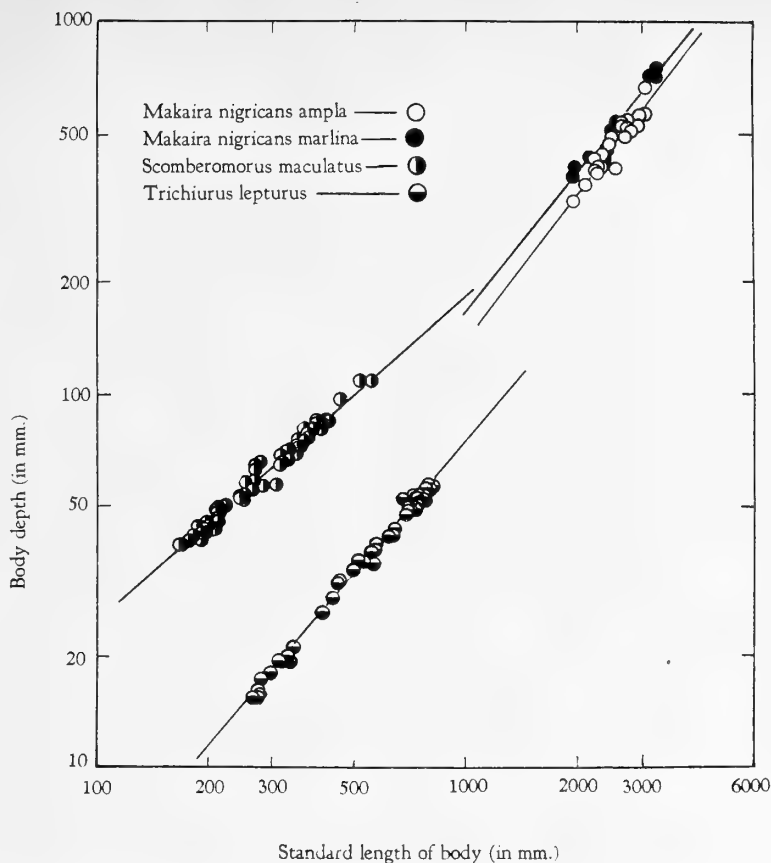
TEXT-FIG. 6. Relative increase of depth in terms of the standard length for the Pomatomidae and the Carangidae. Scale both ways in logarithmic increase.

partition of the growth increments range from 0.75 for *Vomer setapinnis* to 1.25 for *Trachinotus falcatus* (Text-fig. 6). Thus in *V. setapinnis* the body is becoming slenderer to the extent that each unit increase of depth is 0.75 of each unit increase in length. The reverse is true for the positively allometric *T. falcatus*, which becomes relatively deeper as it grows longer. None of the carangids show an ideal isometric condition. *Scomberomorus maculatus* and the allied Trichiuridae and Istiophoridae show relations similar to those exhibited by the Carangidae (Table 2, Text-fig. 7). *S. maculatus*, with a value of 0.87 for  $k$ , grows increasingly slender, whereas *Trichiurus lepturus* ( $k=1.18$ ) and *Makaira nigricans ampla* ( $k=1.32$ ) and *M. n. marlina* ( $k=1.24$ ) shows definitely positive allometric increases in depth.

The significance of such trends may be correlated with the total size that the fish attain and with the value of the gradient for the deposition of weight. According to Glaser (1938) form is of prime importance

and therefore the usefulness of an organ and the adaptiveness of an organism to its environment are to some degree functions of the weight. Changing proportions place upon the organism the necessity of coping with the environment in a constantly differing way. If the environment does not directly affect the direction of growth of the various dimensions, selection in the course of evolutionary change must adjust these factors to maintain an efficient mechanism for the locomotion of the fish as its body weight increases. With an increase in the relative bulk of the fish (i.e., when  $n>3.00$ ) there must be an increase in one or more of the transverse body dimensions. Of the species studied, all those which become relatively heavier with increased length, namely *Trachinotus carolinus*, *T. falcatus*, *Trichiurus lepturus*, *Makaira nigricans ampla* and *M. n. marlina*, also become relatively deeper (compare values of  $n$  in Table 1 with values of  $k$  in Table 2).

All species studied show positive allometry for the relationship of width to length (Table



TEXT-FIG. 7. Body depth relative to body length for the Scombridae and the allied Trichiuridae and Istiophoridae. Logarithmic plotting both ways.

3). They grow in such a manner that the width increases at a proportionally greater rate than the length (Text-figs. 8-11). Thus fishes (*Scomberomorus*, *Selene*, *Vomer*, or *Caranx*) which become relatively lighter ( $n < 3.00$ ) must do so through a relative decrease in depth.

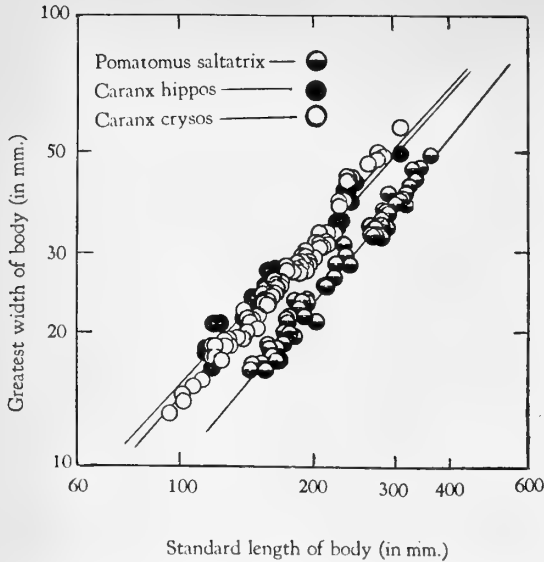
In all the genera, with the exception of *Trachinotus*<sup>5</sup>, the differential growth in width proceeds more rapidly than the growth in depth (compare values of  $k$  in Tables 2 and 3), even in *Trichiurus* and *Makaira*, which show a positive allometric increase in each dimension. The change to a heavier fish proceeds more rapidly along the transverse than along the vertical axis (except in *Trachinotus*). In *Trachinotus carolinus* both depth and width become proportionally greater than length, but the depth maintains a steeper gradient of growth than does the width.

The species studied also show significant

resemblances and differences in the value of the coefficient  $b$  (Tables 2 and 3). In general this value is lower in the more specialized forms (*Makaira nigricans ampla*, *M. n. marlina*, *Trichiurus lepturus* and *Trachinotus carolinus*) than in the more deep-bodied, compressed species. For example, in *T. lepturus*  $b = 0.022$  for depth and 0.0025 for width, whereas in *Vomer setapinnis*  $b = 1.97$  for depth and 0.057 for width.

In general there is a negative correlation between the values of the coefficients  $a$  and  $b$  on the one hand and the values of the exponents  $n$  and  $k$  on the other hand (Tables 1-3). This correlation holds particularly well when the comparison is made between species of the Carangidae and between those referred to the Scombridae, Trichiuridae and Istiophoridae. In biological terms, the species which are the deeper and the wider initially become relatively slenderer and thinner with age, and *vice versa*. In the species studied, therefore, the body form is the more diverse in the young stages, and what might be called an interspecific regulation

<sup>5</sup>The value for  $k$  for the relation of width to length in *T. falcatus* could not be determined because of the large error involved in measuring the small fish which alone were obtainable.



TEXT-FIG. 8. Body width relative to standard body length plotted logarithmically both ways.

in growth tends to mold the adults into a more uniform and conventional fish-form.

#### RELATIVE GROWTH IN RELATION TO PHYLOGENY AND SYSTEMATICS.

The growth intensity of the body as a whole is being distributed according to an orderly system of growth gradients (Thompson, 1917; Huxley, 1932). Each species of scombriform fish here analyzed has been shown to possess an individual and specific pattern of growth, and the relative changes in depth and width have indicated certain similarities for closely related species. It is our purpose to evaluate these specific growth gradients and determine whether or not there is an interspecific trend into which these individual growth gradients will fall.

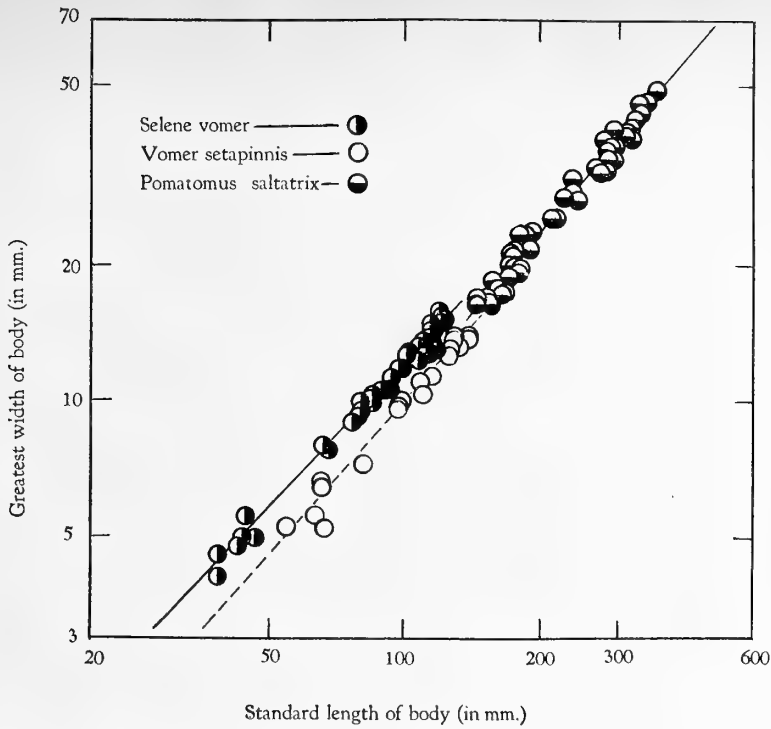
Such allometric growth analysis has been used by other workers to indicate trends in evolutionary growth-partition. Hersh (1934) has pointed out that evolution in the Titanotheres proceeds by constant change in the proportion of dimensions as the size of the species increases. In some skull relations, all the species show a uniform relation between  $b$  and  $k$  and a single straight line curve is obtained, while for other relations a set of curves, each distinct for a genus, results. The differences within any curve are apparently due only to differences in size that the species within a group curve attain. Each curve is based entirely upon measurements of adult individuals and the ontogenetic growth constants are not considered. Similar results have been obtained with the horses. All fossil and modern horses show a distinct group trend with reference

to the muzzle length-total skull length relation (Robb, 1935a), while for the relation between the length of the splints and the length of the cannon bone, two distinct bands are produced, one for the four-toed and three-toed horses and the other for the one-toed forms (Robb, 1936). The horse is characterized by a progressive increase in body size from the Eocene on and, therefore, these curves represent stages in geological time. In the horses the ontogenetic curves are of the same value as the evolutionary group curve (Robb, 1935b). Lumer (1940) has shown that various tribes of dogs may be separated upon their different allometric trends, but here again, as in Hersh's study, no indication of the ontogenetic development is given.

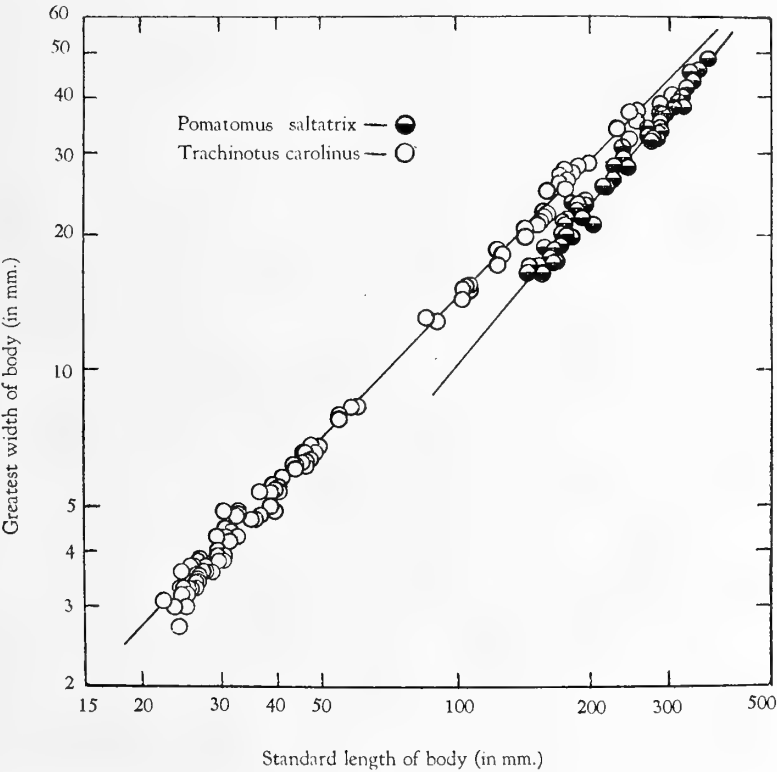
When orthogenetic trends are not present the group curve will represent merely averages of the ontogenetic curves. In this study of scombriform fishes, species within the same genus show distinctly different growth constants. Evolutionary relative growth (which makes use solely of adult measurements) should, in the strict sense, be applied only to groups where the larger species recapitulate in their development the body proportions of the adult stages of smaller species.

The scombriform fishes continue growing throughout life (with body proportions constantly changing) and no definite mature stage can be selected for an evolutionary comparison. Furthermore there is evidence that this group has numerous phyletic lines. Therefore, in order to set up a phyletic system for these fishes (or for any group that does not show an orthogenetic trend) on the basis of relative growth data, the ontogenetic growth constants must be considered. There ought to exist among the members of a genus, or of a higher group, similar trends in these growth constants. That such trends exist in the scombriform fishes is indicated below.

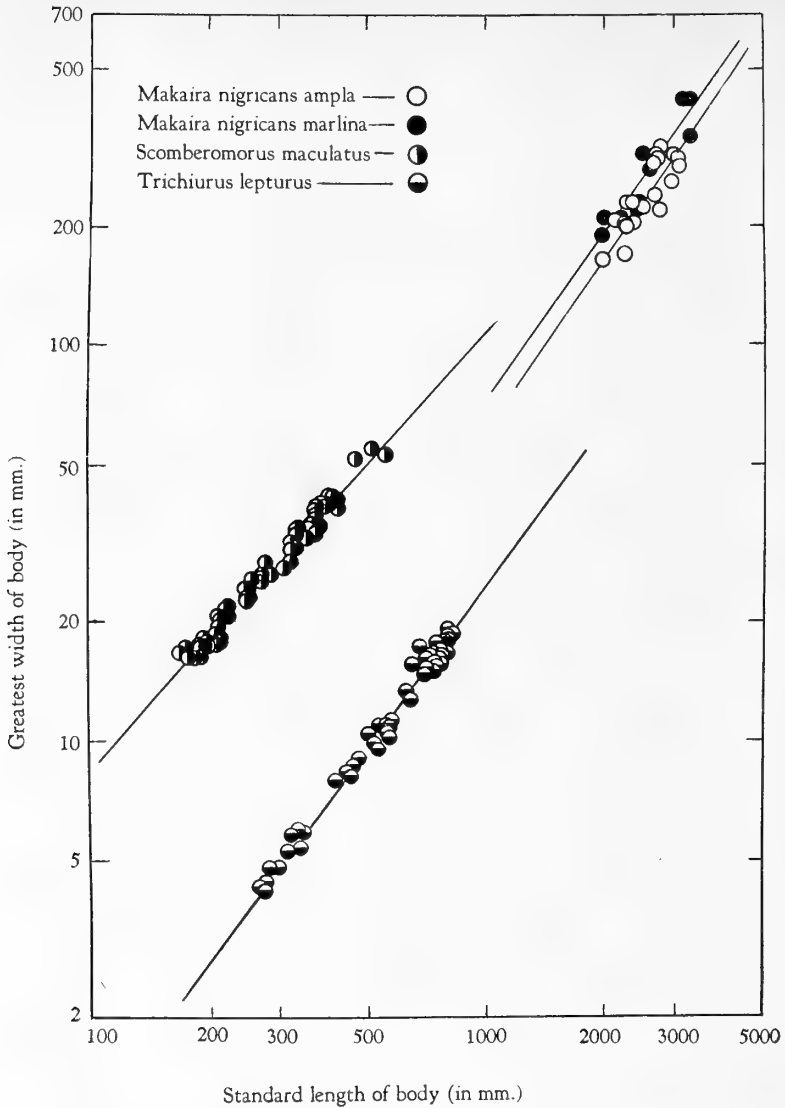
If the values of  $k$  for the growth partition of width and depth (each relative to length) are plotted against each other (Text-fig. 12), it is possible to observe the interspecific trends of the gradients. Since these trends exist, it becomes important to determine whether the ontogenetic change in proportions, characteristic of each species, is a clue to their phylogenetic relationships. Some evidence favorable to this view has been obtained. The lines obtained by the changes in the intensity of the growth constants divide the Scombroidei into two major groups—on one hand the Scombridae with the allied Trichiuridae and Istiophoridae, and on the other the Carangidae (this point is further discussed below). In the scombroids there is a general tendency from the central mackerel type in the direction of



TEXT-FIG. 9. Increase of width relative to length; logarithmic plotting both ways.



TEXT-FIG. 10. Greatest width of body relative to the standard body length; logarithmic plotting both ways.

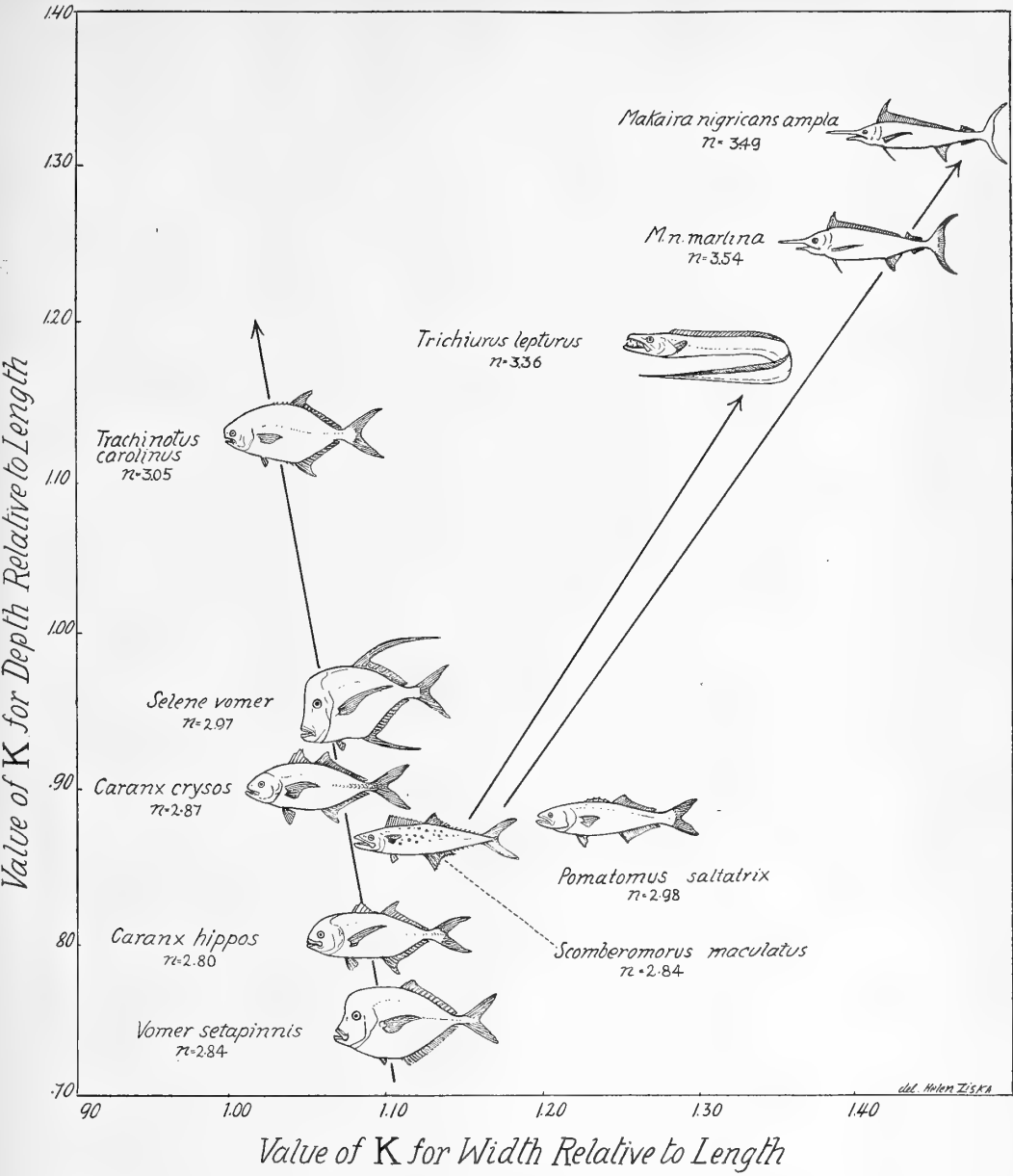


TEXT-FIG. 11. Increase of greatest width of body with increase of standard length; both variables plotted on a logarithmic scale.

the elongate forms. The gradient ( $k$ ) for width increases as does that for depth, but in the sequence to the specialized mackerel-like types, the increase for the depth is slightly greater than that for the width. For the Carangidae this tendency is even more marked and results in a complete reversal of the intensity of growth in the transverse and vertical dimensions. Per unit increase the width shows greater growth than the depth in *Vomer setapinnis* and there is a general trend in the direction of *Trachinotus carolinus* where the depth now maintains greater increase than the width. These are broad tendencies, as shown here,

and it should be emphasized that for a more exact phylogenetic scheme, where generic and specific tendencies may be followed, more complete data are necessary.

There is a pattern of growth that is individual for each species but each pattern conforms, nevertheless, to a general scheme indicative of the trends of the larger groups. This seriation of the gradients of growth for the species suggests that phyletic lines can be determined by the allometric method and that change in the growth gradients is the mechanism by which the course of evolution proceeds. If so, the mathematical analysis of the interspecific changes in the



TEXT-FIG. 12. The various species of the Scombroidei plotted according to the values of  $k$  for depth relative to length and width relative to length. Both ordinate and abscissa are for increasing units of  $k$ . The value for the increase of weight relative to the length ( $n$ ) is given for each species.

proportions and form of the organism should be a further tool to the phylogenist and systematist.

The divergence of the gradients for the Carangidae on the one side and the Scombridae and immediate allies on the other (Text-fig. 12) is in harmony with the view that these gradients reflect phylogeny. The sepa-

ration of lines for the carangids and scombroids indicate broadly the phylogenetic division accepted by many workers, either as separate lines within the Scombroidei or as independent modifications of a typical percomorph (serranid) stock. The Carangidae are grouped with the Scombridae and related families into a single suborder, the

Scombroidei, by many authorities, including Jordan and Evermann (1896, p. 862), Starks (1909, 1910) and Gregory (1933, p. 300). In their view the carangids, although possessing many percoid characters, appear to be even more closely related to the true scombroid families and can therefore be bracketed into a percomorph suborder, the Scombroidei. Tate Regan (1909, 1929, p. 321), however, refers the carangids to the percoid suborder and the true scombriforms to a separate suborder, the Scombroidei.

The primary fusiform body, illustrated by the mackerels, is a specialized stage away from the general, although somewhat deep-bodied, percomorph types. *Scomberomorus maculatus* has the initial growth index characteristic for the fusiform body ( $a = 0.0000288$ ). This mackerel, however, maintains the early fusiform condition as it grows ( $k$  for depth = 0.87, Table 2). The most advanced stage away from the primary fusiform body is the elongate type represented by *Trichiurus lepturus*. The fusiform condition has been lost by excessive elongation ( $a = 0.0000000674$ ). *Makaira* may be classified as a specialized fusiform type. The initial growth index is very low ( $a = 0.000000161$  for *M. n. ampla* and  $0.000000118$  for *M. n. marlina*) and like *Trichiurus* they are very slender fish early in development. They attain their fusiform condition only through the intense gradients at work during their growth.

There is no evidence of any Scombridae appearing until the Eocene, when they are already fusiform, primarily elongated forms with a vertebral number of 30-50. In this group total length has increased due to the increased number of vertebrae (the primitive acanthopterygian number is 10 + 14). The increase in vertebral number would seem to be a normal method of assuming the fusiform condition early in ontogenetic growth and maintaining it throughout life, providing there was no excessive increase in depth. The geological evidence would place the mackerel group as an early (Eocene) offshoot of its percomorph ancestor.

The mackerels illustrate the first step toward the elongated form represented by the Trichiuridae. The independent trichiurid line begins with *Ruvettus*, which is close to the mackerel type, and follow through by successive stages in modification and elongation until the end stage represented by *Trichiurus* is reached. *Trichiurus* is secondarily elongated (its vertebral number is 159).

The marlins, with 12+12 or 12+13 vertebrae, are already specialized with respect to this deviation from the basic percomorph pattern of 10+14. Early in their post-metamorphic development they are extremely long-bodied as indicated by their initial growth index. These fish lose their early

slenderness and attain a thick-fusiform streamlined condition, during their growth, through the maintenance of steep gradients; that is, through increase in the gross size of their parts. Thus the Istiophoridae present a distinct line of specialization resembling that of the Scombridae, in that both have a fusiform body—attained in the marlins during ontogenetic growth but present, however, at the beginning of and maintained during post-metamorphic growth in the mackerels. We are dealing with two widely divergent lines of evolution, each with striking differences (in vertebral number and growth constants) but nevertheless with considerable anatomical evidence to indicate a common heritage.

The bluefish (*Pomatomus*) has been considered the connecting link between the Serranidae and the Carangidae (Tate Regan, 1909), because of the intermediate character of its skull, general body form, caudal peduncle and caudal fin. In its external body form, however, it seems to have assumed the specialized contours of the fusiform mackerels, with which other authors have classified the genus. Its vertebral number still remains the primitive 10+14 percomorph number, but its form of body appears to be a case of parallel development of the fusiform type of body correlated with a predatory habit. The change has not been incurred in the mackerel manner, by an increase in vertebral number, but rather as in *Trachinotus* by a modification in relative growth (the initial growth index =  $0.0000229$  for *Pomatomus*). Since deepening of the body does not take place during growth as it does in *Trachinotus* ( $k$  for depth = 0.88 rather than 1.13, Table 2), the fusiform external mackerel condition established in the young stages of growth is maintained. *Pomatomus* could have well arisen from a serranid ancestor independently from the carangids—but perhaps from the same basic stock.

The relative growth method does not indicate the direction of phyletic lines and thus creates some difficulty in interpreting the line of carangid evolution. Since the increasing specialization of the scombroids appears to follow the line of divergence as indicated by the allometric growth method (see Text-fig. 12), such a trend may also be characteristic of the carangids. The value for the initial growth index is high for the deep-bodied *Selene vomer* ( $a = 0.0000483$ ) and *Vomer setapinnis* ( $a = 0.0000648$ ) but these fish become slender as they grow in size. *Caranx hippos* and *C. crysos* show the same relations for their post-metamorphic development. These fish can be designated primary deep-bodied types, regardless of whether the deep body of the early stages recapitulates the deep body of extinct ancestors or is a juvenile adaptation. *Trachino-*



*tus carolinus* shows a distinctly opposite trend. It is slenderer and more fusiform in the early stages of growth ( $a = 0.0000264$ ) but becomes deepened during growth ( $k$  for depth is 1.13). It can thus be designated a secondarily deepened type.

Apparently two interpretations of this evidence are possible. These differences in the growth relations might well serve as evidence either that *Trachinotus* has been independently derived from the typical carangid line, or, as Gregory (1933) maintains, it is a longer-bodied derivative of the more primitive deep-bodied compressed types. The seriation as seen in Text-fig. 12 would seem to favor the interpretation that *Trachinotus* is a more specialized carangid in the direct line of ascent from the deep-bodied *Selene*, *Vomer* and *Caranx*. The initial growth index for *Trachinotus* is similar to that for the specialized *Scomberomorus* (Table 1). *Trachinotus* is only fusiform early in its post-metamorphic growth, but reverts to a deep-bodied condition during its ontogenetic growth. The Scombridae by increasing the number of vertebrae, have taken what seems to be a more normal and advanced method of assuming the fusiform condition. Thus their manner of attaining the fusiform condition was a more complete break from their ancestral type than *Trachinotus* was able to accomplish from the typically deep-bodied carangids or deep-bodied carangid ancestors, if it has come off independently from the carangid ancestors.

#### SUMMARY.

Relative growth methods are used to determine the relation between weight and body form in several fishes generally classed in the suborder Scombroidei.

The cube relationship between weight and length is only an approximation and in most of the species analyzed is not even closely realized. An allometric increase or decrease of weight in relation to length is correlated with the fact that the dimensions of the body are not necessarily a linear function of length. This non-linear relation may hold even when an isometric weight-cube-length condition is realized, for the changes in different dimensions may be compensatory.

Fish that attain a greater total size show a smaller bulkiness (initial growth index) early in their post-metamorphic growth, whereas the deep-bodied shortened fish have greater relative bulk at this stage of their growth. However, fish that are slim early in ontogenetic development tend to possess a high positive allometric distribution of weight during growth, and *vice versa*. This inverse relationship of the initial growth index to the growth constant is exponential and may be of some value in determining phylogenetic trends.

The depth in some species shows positive allometry, in others it is negative. All species studied, however, show positive allometry for the relationship of width to length. It is thus indicated that fishes which become relatively lighter during growth can do so only through a relative decrease in depth.

The differential growth in width proceeds more rapidly than the growth in depth in all the species with the exception of *Trachinotus carolinus*, where this condition is reversed. Thus, in the majority of scombriform fishes studied, the change to a larger fish proceeds more rapidly along the transverse than along the vertical axis.

In general there is a negative correlation between the values of the initial growth index and the values of the growth constants for the dimensional proportions. Species that are deeper or wider initially become relatively slenderer or thinner with age, and *vice versa*.

Closely allied members of the various families have similar coefficients of growth partition, but specific differences are nevertheless maintained.

The interspecific trends of the ontogenetic growth constants suggests the possibility that phyletic lines can be determined by the allometric method. The pattern of growth that is individual for each species seems to conform to a general scheme indicative of the evolutionary trends of the larger groups. Differences in relative growth trends within the Scombroidei of earlier authors characterize separate groups that have been or might be regarded as representing either separate divisions within the Scombroidei or entirely independent parallel phyletic lines.

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## 13.

## A Record of the Successful Breeding of the Quetzal (*Pharomachrus mocinno costaricensis*) in Captivity.

CHARLES CORDIER

In March, 1942, I had the good fortune to meet in San José, Costa Rica, Señora Amparo Zeledon, widow of the well-known ornithologist who died a few years ago.

At that time I was starting on a collecting trip having as its objective the capture of the Bare-necked Umbrella Bird (*Cephalopterus ornatus glabricollis*) and other rare birds for the New York Zoological Society.

It was with considerable elation that I noticed at Señora Zeledon's home a large, well-planted aviary, approximately 30 × 15 × 10 feet, in which was a pair of Costa Rican Quetzals, *Pharomachrus mocinno costaricensis*, in superb condition. The male trailed behind in its flight a pair of upper tail coverts nearly a yard long. Subsequently I was able to purchase this pair and the birds are now (February, 1943) on exhibition in the New York Zoological Park, together with several other Quetzals.

The most interesting part of my discovery was that Señora Zeledon told me that the Quetzals had reared young successfully on two occasions and that she had made notes of these events at the time. She was kind enough to lend me her notes, which I have translated and reproduce herewith:

### SEÑORA ZELEDON'S NOTES ON THE BREEDING OF THE QUETZAL.

"We noticed the young bird peeping through the entrance hole on August 8, 1940, and on the 12th it left the nest.

"Both male and female were feeding it as long as it was confined to the nest, but once outside, only the mother cared for it, feeding it earthworms (Of all things—Translator) in the morning, and fruit (By which is meant cut-up little plantains known locally as "guinea"—Translator). On the 16th of the same month it fed itself for the first time. I suppose the birds started nesting at the end of June.

"The tree trunk in which they nested had been in the aviary for more than two years, exposed to the weather, before they showed any interest in it, the male preferring to enter a bigger, irregularly-shaped hole in the wall forming one side of the aviary. The

female, however, would only reluctantly go near it, the entrance hole probably being too wide. Fortunately they decided on nesting in the tree trunk after two long years, the wood having become soft enough to be worked on by them.

"The male moulted at the end of August and lost its long tail coverts at the end of September.

"The plumage of the young bird at the moment it left the nest was uniform coffee-color, except the wing coverts which were green.

"Both parents had been kept for three years in the big aviary and previously for two years in a much smaller aviary in which they would get very wild as soon as approached. In the big enclosure they are quite steady and take no notice of visitors. The pair was composed of a young male and an adult female purchased from the natives.

"February, 1941: The male, already in good plumage, started to enter the nest in the middle of February and to clean it out, carrying loads of dust in his breast feathers which he would shake out, once outside. Both started uttering their calls and the female entered the nest some days later, mornings and afternoons. Both adults started chasing the young Quetzal from the vicinity of the nest and stayed continuously near it, even in March.

"On March 31, 1941, I noticed the female coming out of the nest to let the male get in. Shortly afterward the male came out and the female re-entered.

"April 19: Today I had the gardener trim the trees in the aviary and he noticed two young birds in the nest, maybe 8 days old.

"Five days later we found a dead young Quetzal on the ground. One side showed signs of having been injured. Possibly the birds got frightened when the gardener worked in the aviary and threw one of the nestlings out.

"The young Quetzal, reared the previous nesting season, is still being relentlessly persecuted by its parents. On Friday, May 2, they bit it almost to death. I took it out, did my best to cure it, but found it dead the

following day. I had made the mistake of putting it back in the aviary. Even when it was lying dead on the ground, the female would swoop furiously down on it.

"On May 12, 1941, this season's young Quetzal could be seen at the nest hole. It left the nest on May 18, early in the morning. Male and female re-entered the empty nest several times that day."

#### FURTHER OBSERVATIONS IN THE FIELD.

On discussing the birds' performance, Señora Zeledon said she believed she knew why the Quetzals waited two years before nesting. She thought the wood in the tree trunk was too hard and they could not work it and shape it to their liking. In 1942 she had the old tree trunk replaced but no attempt at breeding was made, the wood probably again being too hard.

I measured the old trunk and found it to have a diameter of about 12 to 13 inches. The nesting hollow was approximately 9 inches in diameter. At the bottom was a shallow cup hollowed out, leaving a rim all around of a width of about 2 inches. The lower rim of the entrance hole, almost 5 inches in diameter, was about 6 inches from the rim of the cup.

Any future attempt at breeding should take into consideration the condition of the log, which should be so well rotted throughout that bits can be pried off with the fingernail, and should have an entrance hole and nesting cavity smaller than the measurements given above. The birds will accommodate it to their liking themselves. It would also be a good plan to wet the log thoroughly from the outside, with a hose, daily, to reproduce natural conditions.

Quetzals breed in cloud forests which are

dripping wet almost the year around. While in Costa Rica I found two nests at an altitude of 4,000 feet. One was located deep in the cloud forest in a tree stump about 15 feet tall, so rotten that it swayed when a finger was pressed against it. The diameter of the stump was at most 9 inches, which goes to show that occasionally the Quetzal takes to cramped quarters. The entrance hole was about 12 feet from the ground. I caught the male, who was brooding inside, by walking noiselessly up to the nest and covering the hole with a butterfly net on a short pole. This was in the month of June.

The second nest was situated in an enormous tree trunk, charred by fire and standing in a clearing. The entrance hole was a good 20 feet from the ground. The native who climbed up to it risked his neck by doing so. The nest was deep. He brought up two eggs, the size of pigeon's eggs, uniformly blue in color. He replaced them but the birds abandoned the site. The natives said that they invariably do this when the eggs have been touched.

At first I thought the Quetzal lives in association with the great woodpecker, whose abandoned nest he would take over and accommodate to his liking, but later I was not so sure of this. Quetzals breed up to 10,000 feet and at the higher levels the big woodpecker is not found, being replaced by a medium-sized woodpecker, so that the Quetzal would have to accommodate a much smaller nest.

Despite the Quetzal's diminutive feet and short bill, he must be a good carpenter. I once observed in Guatemala a Red-bellied Trogon hollowing out, with feet and bill, an occupied termite nest, and these are quite hard.

## 14.

The Occurrence of Leeches, *Ozobranchus branchiatus*  
(Menzies), on Fibro-Epithelial Tumors of  
Marine Turtles, *Chelonia mydas* (Linnaeus).

ROSS F. NIGRELLI

New York Zoological Society

&amp;

G. M. SMITH

Yale Medical School and New York Zoological Society

(Plates I-III).

In the course of study on parasites of *Chelonia mydas*, Nigrelli (1941) reported the presence of large numbers of leeches, *Ozobranchus branchiatus* (Menzies, 1791), on fibro-epithelial tumors removed from turtles caught off the West Coast of Florida and sent to us by Mr. Stewart Springer. The leeches were previously described from the same host by MacCallum and MacCallum (1918) but these investigators did not mention the tumors.

The tumor masses were removed from the neck and eyelids of turtles and on a piece one-half inch square as many as fifty leeches in various stages of growth were counted. The largest of these ectoparasites measure about 10 mm. in length and 5 mm. in width (Fig. 1). They are strongly contracted as the result of preservation, and it is assumed that when alive and fully expanded they must be at least three times as long. There is a powerful sucker at the posterior end of the animal and the body possesses lateral filaments which are described as gills (Fig. 1, G). The mouth is small, round in shape and furnished with smooth thick lips. On the dorsal side of the anterior region may be found two eye spots (Fig. 2), although these structures are not always demonstrable. An examination of the intestinal contents shows that these annelids feed almost entirely on the blood of the host.

The tumors are of the same type described by Smith and Coates (1938). The tissues appear as papillary growths or as round fibromata arising from the skin. The leeches are attached to the tumors by their posterior suckers and on the papilloma they are usually found buried deep in the crypts formed by such growths (Fig. 2). In many instances it is difficult to distinguish be-

tween the growth proper and the leeches (Fig. 3).

Microscopically, the papilloma shows a definite thickened epithelium with a certain amount of keratin formation (Figs. 5, 6, 7). The stroma is highly vascular, especially in regions where the leeches are attached (Fig. 7). The fibromata is characterized by a dense, intermingling fibrous growth, covered at the surface with a normal amount or slightly thickened epithelium. Nests of leeches also have been found attached on these smooth growths (Fig. 4).

The etiology of the growths is still unknown. Smith and Coates (1938) discuss the possibility of a viral or parasitic agent. Later (1939) they reported the presence of trematode eggs in many of the tumors examined. These eggs were eventually identified by Smith, Coates and Nigrelli (1941) as those of blood flukes originally described by Leared (1862) as *Distomum constrictum*. According to Smith and Coates (1939), "It is probable that ova are deposited in pre-existing vascular tumor tissue by the migrating blood flukes, and remain there without affecting the subsequent course of the growth." They pointed out, further, that the localization of ova in the stroma and in the venous or lymphatic spaces of the turtle tumors is somewhat similar to the condition in the tissues of the urinary bladder in human bilharziasis. "Such an infection of the human bladder, as is well known, may result in papillomatous and malignant changes."

Just what role the ectoparasitic annelids play in the development of these turtle tumors is not certain. They may act as vectors for viral or other parasitic forms that may be the causative agent, although histological

examination of a number of sectioned and stained leeches showed no evidence that they are involved in the transmission of helminthic parasites of the turtles. However, it is altogether possible that the leeches may have some effect on the subsequent growth of the fibro-epithelial tumors. It is known that they feed on the turtle's blood; the latter is prevented from clotting by the action of hirudin. Such a continued flow of blood makes an excellent medium, supplying the necessary nutriment for these slow growing tumor cells. That hirudin, *per se*, may have some effect on the growths is indicated by certain experiments reported in the literature involving the use of heparin. Thus, Ligneris (1930) found that transplantations of melanoma of angora goat on homologous animals were successful only when heparin-goat-plasma was used as a nutritive and protective medium surrounding the transplanted tumor particles. Zakrzewski (1932) showed that better proliferation of tissues was obtained when heparin was added to blood serum used as the culture medium.

#### SUMMARY.

1. Leeches, *Ozobranchus branchiatus* (Menzies, 1791), were found associated with fibro-epithelial tumors of marine turtles, *Chelonia mydas* (Linnaeus).

2. The role of the buccal secretion of the leeches (hirudin) is discussed in connection with the growth of the tumor tissues.

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#### EXPLANATION OF THE PLATES.

##### PLATE I.

- Fig. 1. Photograph of leeches removed from turtle tumors. **G**, gill filaments; **S**, posterior sucker. About 4 ×.
- Fig. 2. Leeches buried in papilloma crypts. Note minute eye spots. About 3 ×.

##### PLATE II.

- Fig. 3. Nest of leeches among the papillae. Some of the smaller leeches are difficult to distinguish from growth proper. 3 ×.
- Fig. 4. Nest of leeches, in various stages of development, on smooth fibromata of the turtle.

##### PLATE III.

- Figs. 5, 6, 7. Photomicrographs of the turtle tumor. Note relationship of leech to tumor. The stroma of the tumor is highly vascular. About 5 ×.



FIG. 1.



FIG. 2.

THE OCCURRENCE OF LEECHES, *OZOBANCHUS BRANCHIATUS* (MENZIES), ON FIBRO-EPITHELIAL TUMORS OF MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).







FIG. 3.



FIG. 4.

THE OCCURRENCE OF LEECHES, *OZOBANCHUS BRANCHIATUS* (MENZIES), ON FIBRO-EPITHELIAL TUMORS OF MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



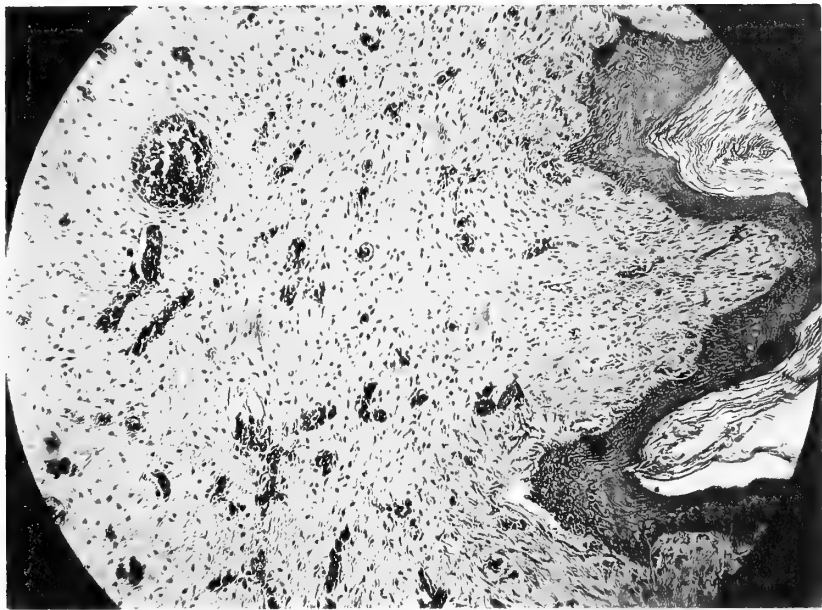


FIG. 5.



FIG. 6.

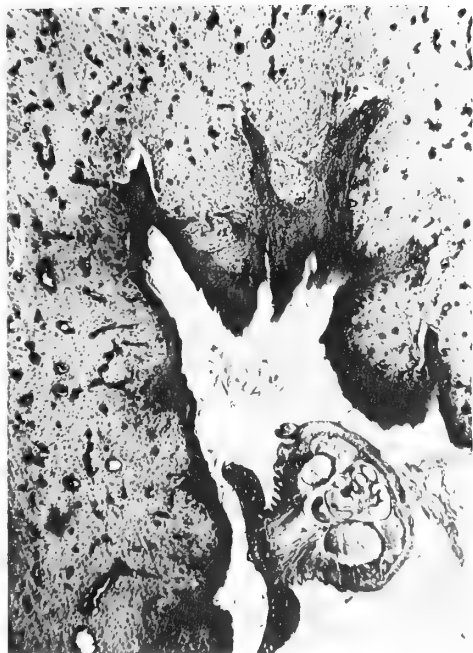


FIG. 7.

THE OCCURRENCE OF LEECHES, *OZOBANCHUS BRANCHIATUS* (MENZIES), ON FIBRO-EPITHELIAL TUMORS OF MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



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## 15.

# On the Relationship of Some Common Fishes as Determined by the Precipitin Reaction.

DOUGLAS G. GEMEROY

From the Zoological Laboratory, Rutgers University

(Text-figures 1-7).

## INTRODUCTION.

It is generally agreed that the goal of taxonomy is the tracing of phylogenetic relationships and since the time of Darwin the emphasis in classification has been on the phylogenetic method in taxonomy. The chief source of data in phylogeny and classification has been morphological, and there is a need of some independent source of data with which to check the morphological interpretation. Such an independent source is available in the serological or biochemical constitution of animal proteins.

Nuttall's pioneer studies with the precipitin reaction applied to the determination of animal relationships have been followed by many others in both plants and animals, Mez and Ziegenspeck (1926); Landsteiner (1936) and others whose work is covered in the recent review of Boyden (1942). In the thirty-nine years since the publication of Nuttall's "Blood Immunity and Blood Relationship," progress has been made both in results and their interpretation, but the importance of serological data in taxonomy and phylogeny is still a controversial matter. In

order to provide further data from which a conclusion might be drawn as to the relative importance of the serological method of attack on phylogeny and taxonomy, a study of the relationships of common fish was undertaken, using the old or common precipitin technique of the ring test and the new photron'er (photronreflectometer) methods introduced by Libby (1938). Such an approach is both quantitative and objective and is independent of morphology which it may complement and whose findings it may check. Further it may shed new light on many groups whose relationships are still uncertain with the methods available to morphology. The present paper represents the results of more than 500 tests upon the blood sera of 31 species of fresh water and marine fishes.

## MATERIALS AND METHODS.

## I. Sources of Serum.

The sera for the data of the present paper were procured from the species of fish listed below. Both common and scientific names are given.

Common Name	Scientific Name
Lamprey	<i>Petromyzon marinus</i> (Linnaeus)
Common Shark	<i>Carcharhinus</i> sp.
Yellow Shark	<i>Hypoprion brevirostris</i> Poey
Scyllium	<i>Scyllium canicula</i> (Linnaeus)
Dog-Fish	<i>Squalus acanthias</i> Linnaeus
Barn-door Skate	<i>Raja laevis</i> Mitchill
Eagle Ray	<i>Aetobatis narinari</i> (Euphrasen)
Sturgeon	<i>Acipenser rubicundus</i> (LeSueur)
Garpike	<i>Lepisosteus osseus</i> (Linnaeus)
Bowfin	<i>Amia calva</i> Linnaeus
Tarpon	<i>Tarpon atlanticus</i> (Cuvier and Valenciennes)
Brook Trout	<i>Salvelinus fontinalis</i> (Mitchill)
Rainbow Trout	<i>Salmo irideus</i> Gibbons
Brown Trout	<i>Salmo fario</i> Linnaeus
Carp	<i>Cyprinus carpio</i> Linnaeus
Buffalo Fish	<i>Ictiobus cyprinella</i> (Cuvier and Valenciennes)
Red Horse or Mullet	<i>Moxostoma aureolum</i> (LeSueur)

Catfish	<i>Ameiurus lacustris</i> (Walbaum)
Gaff-topsail Catfish	<i>Bagre marinus</i> (Mitchill)
Sea Catfish	<i>Galeichthys felis</i> (Linnaeus)
Pike	<i>Esox lucius</i> Linnaeus
Muskallunge	<i>Esox masquinongy</i> Mitchill
Barracuda	<i>Sphyraena barracuda</i> (Walbaum)
Dolphin or Dorado	<i>Coryphaena hippurus</i> Linnaeus
Black Bass	<i>Micropterus dolomieu</i> Lacépède
Large Mouth Bass	<i>Huro floridana</i> (LeSueur)
Rock Bass	<i>Ambloplites rupestris</i> (Rafinesque)
Blue Gill Sun Fish	<i>Helioperca incisor</i> (Cuvier and Valenciennes)
Perch	<i>Perca flavescens</i> (Mitchill)
Pickereel	<i>Stizostedion vitreum</i> (Mitchill)
Kingfish	<i>Menticirrhus americanus</i> (Linnaeus)

## II. Collection of Serum.

The blood sera of the different fish listed above were obtained from various sources. The fresh water species were procured from Northern Ontario, the State Fish Hatchery at Hackettstown, New Jersey, the New York Aquarium and live fish markets in New York City. The salt water species were procured from a number of the different Biological Laboratories along the Atlantic and Gulf Coasts.<sup>1</sup>

## III. Handling of Serum.

Two methods are used regularly to obtain blood from fish.

1. By syringe direct from the heart.
2. By drip method from the caudal artery.

With the fresh water species the first method was used throughout, while with the salt water species the second method was used in all cases except the shark, where the pericardial cavity was cut open and the blood allowed to drain into a receiving bowl directly. All bloods collected were allowed to clot for a period ranging from 6 to 12 hours. The serum that had been expressed from the clot by this time was poured off and centrifuged at 2,500 r.p.m. until free from cellular elements. In all cases where the serum was stored without any preservative it was first filtered through a Seitz filter and then bottled under sterile conditions. The greater portion of the sera collected however, was preserved by the addition of 0.02 ml. of 10 per cent. formalin to every ml. of serum. A few samples collected in the fall of 1940 were preserved by the addition of 1 ml. of 1:1000 merthiolate solution to each 10 ml. of serum. All the formalized sera were kept at room temperature during the course of the investigation, while the native and merthiolated

sera were kept in the electric refrigerator, except when small samples were being used for antisera production or in carrying out the required tests.

## IV. Protein Determinations.

Prior to the use of the different sera in antibody production, total nitrogen and non-protein nitrogen determinations were carried out by the micro-Kjeldahl digestion method of Koch and McMeekin (1929). From these figures the total protein was obtained by multiplying the T. N. — N.P.N. by factor 6.25. For N.P.N. determinations the protein was precipitated with trichloroacetic acid. In the ring test where the end point of the reaction is the standard employed in determining relationships, comparable amounts of protein must be used in the different dilutions of the various antigens to give a quantitative basis for such relationships. In the tests reported here only standard and comparable antigen dilutions have been used.

The protein concentration of the fish sera in gms./100 ml. of serum varied from 1.50 gms. to 5.50 gms. The majority, however, were between 2.5 and 3.5 gms. The N.P.N. concentration in mgms./100 ml. of serum ranged from 20 to 125 mgms. with the exception of the elasmobranchs. Here the highest figures were recorded, being 1,000 mgms. or more in practically all members of this group.

## V. Injection Methods.

Where antisera of maximum specificity are desired a single series of injections is administered. These injections are made on alternate days with the initial injection in all cases being 5 milligrams of protein per kilogram of body weight of the injected rabbit. Each subsequent injection is double the amount of the previous one until four injections in all are given. Where decreased specificity is desired in an antiserum to increase the range of cross reactions, multiple series of injections are required, Wolfe (1935). Preliminary tests with fish blood serum showed that the range of cross re-

<sup>1</sup> The author wishes to thank Drs. C. M. Breder, Jr. and Alan A. Boyden who contributed all the marine species used and Mr. C. O. Hayford, Superintendent of the State Fish Hatchery at Hackettstown, New Jersey, for a number of the fresh water species. He also wishes to express his appreciation to Drs. T. C. Nelson, C. M. Breder, Jr. and Alan A. Boyden for valuable aid and criticism of this paper. Submitted to the Graduate Faculty of Rutgers University in partial fulfillment of the requirements for the Degree of Doctor of Philosophy.

actions in the majority of the antisera made to a single series of injections was rather restricted. To broaden the range of reaction multiple series of injections were employed with three rabbits. In multiple series injections, the initial series is followed after a lapse of one week by a second and even a third series of injections.

Eight days after the last injection, a trial bleeding of the animal was taken to determine whether the antiserum was of desired potency. In all but one case the antisera were sufficiently potent. On the following day the rabbits were anesthetized and all the blood obtainable was drawn directly from the heart by means of a large syringe and transferred to a finger bowl. The blood was allowed to clot in the refrigerator for eight to twelve hours, after which the expressed serum was decanted off, with minimum disturbance to the clot, and centrifuged at 2,500 r.p.m. until clear of cellular elements. The antiserum was then passed through a Seitz filter and bottled under sterile conditions. All the antisera thus treated were stored in the refrigerator at  $4^{\circ}\text{C.} \pm 1^{\circ}\text{C.}$  until needed. In no case where such a procedure was carried out did contamination occur in the refrigerated antisera.

#### VI. Ring and Photron'er Tests.

The ring and photron'er tests were carried out in the usual manner, the technique being that described by Boyden (1942).

#### EXPERIMENTAL RESULTS.

The results of the different tests carried out by the ring and photron'er methods are shown in Tables I, II, III, IV. The percentage relationship found with the various sera used in the heterologous reactions is shown as a per cent. of the homologous tests with both ring and photron'er methods. With the ring test, duplicate readings were taken with all reactions, fresh dilutions of antigen and antisera being made up before the second series of tests was run. The antisera used in the ring tests were diluted 1:1 in all reactions, while with the photron'er they were used in full strength, as it was found in preliminary readings that diluting the antisera 1:4 eliminated practically all the heterologous reactions. Most of the antisera produced by means of a single series of injections were highly specific, hence no dilution was necessary.

Supplementing the tables are representative figures depicting homologous and heterologous reactions through their complete range as recorded on the photron'er, also representative graphs of the ring test showing the per cent. relationship values as determined from the titers of the homologous and heterologous antigens used.

#### Symbols.

A number of symbols are used in the tables and figures; the explanation of which is as follows:

- (Fo)—Antigen was formalized. Where this symbol appears after an antiserum it means that the antiserum was produced by the use of a formalized antigen. In no case was the antiserum formalized.
- (N)—Antigen was used without any preservative in all reactions. Antisera were produced with the native antigen.
- (S3)—Antiserum produced by means of a triple injection series.

#### DISCUSSION OF EXPERIMENTAL RESULTS.

##### I. Technical Considerations.

##### (a) Preservation of antigens with formalin.

As it is necessary to use some type of preservative when antigens are collected in the field, formalin was employed wherever such sera were preserved. From the unpublished data of M. A. Carriker, working in this laboratory, it was found that 0.2 per cent. formalin could safely be used for the field preservation of animal sera. In the present series of investigations, comparative tests were carried out to determine to what extent such treatment had altered the species specificity of the different blood sera. Text-figures 2 and 3 give an indication of the parallel results obtained when formalized and native antisera were reacted with the antigens used in their production. The same group of heterologous antigens show parallel relationship with the antinative and anti-formalized antisera. Such results indicate that the use of formalin as a preservative under these conditions has not altered to any appreciable extent the "relationship" values shown by these two series of elasmobranch blood sera.

##### (b). Comparison of photron'er and ring test methods.

The ring test method of using the precipitin reaction in the determination of animal relationships has been the standard for many years and has been used successfully by many workers in serological investigations. With species that are not too closely related, this method is still valuable, as the range of reactions is great enough to include some distantly related species.

Although very sensitive at low concentrations of precipitated protein, the ring test as commonly performed gives only the end point, with no measure of the degree of reaction at intermediate levels. The photron'er, although less sensitive at the end point, gives a quantitative measure of the degree of reaction at every concentration of

the reacting substances. This instrument is far more effective than the ring test, therefore, where close relatives are involved. The ring test method can be likened to a low power microscope with its broad field of vision, while the photron'er acts like a much higher powered instrument. It pulls apart, as it were, antigens that show no difference in titer with the ring tests.

When the two methods are used in the precipitin reaction, one complements the other. Where rather widely separated species are being tested, the photron'er is, as a rule, highly specific and may not show any reaction in such cases. Where the ring test is employed and only the end point of the reaction is determined, the sensitivity of this method is apparent. By its use, cross reactions that can not be determined with the photron'er are established with the ring tests.

## II. *Bearing of results on the problem of fish relationships.*

### (a). *On animal relationships in general.*

As a fundamental approach in studying the diverse types of living organisms, the problem of the systematic relationship between such groups is of prime importance. The term animal relationship can be used to express any association between animals, but in its common usage it denotes systematic or genetic relationship. Although the principles on which animal relationships are based are by no means agreed upon by all taxonomists and morphologists, those outlined by Boyden (1942) seem to be the logical choice as a foundation for any particular attack on the problem of classification. Systematic relationships based upon conservative hereditary traits involve genetic relationship. To distinguish non-essential from essential criteria on which the grouping is based, should be the prime object. Those characters which most faithfully indicate a common heritage, will best serve as guides to the study of animal relationships.

Characters are not equal in this respect, however, for although the vast array of structural characters is primarily due to heredity in their mature expression, they may be affected by environment. By such interaction they may or may not help to reflect the common ancestry. Besides the morphological, both chemical and physiological characters are also determined primarily by inheritance. Some of these may also be modified in their mature expression by environmental influences. On the other hand, certain physiological characters, such as the blood groups, so far as is known, are determined so completely by inheritance as not to be affected by environment at all. On such a basis, it seems appropriate to use all kinds of conservative characters, morphological,

biochemical and physiological, the choice of such characters depending on the relative constancy with which they indicate a common inheritance.

If it be true that the chemical nature of an organism, as well as its morphological expression, is determined primarily by inheritance, then morphology alone is not a complete basis for determining the degree of animal relationship. The evidence indicates that chemical similarity of proteins of various animal species denotes the relationship of such species, the closer the similarity of such proteins, the closer the degree of genetic relationship between them, Boyden (1942). The problem of classification is extremely complicated, but with a better understanding from the newer methods employed, it has much greater possibilities of achieving a truly natural classification than was formerly believed. In such a problem, then, we must be assured that the characters picked are conservative and any classification based on the nature of the organism should use all such characters and not confine itself to morphological expressions alone.

As a physiological character not appreciably affected by the environment to any extent, the blood sera of various animal species seem to be highly promising. Moreover, the conservativeness of this character is assured by means of the antibody mechanism existing in the organism, which apparently compels serum proteins to change but slowly. Since the discovery of the precipitin reaction by Kraus (1897) and the statements of Wells (1929) and Landsteiner (1936) that the chemical similarity of proteins can be demonstrated, many studies of the relationships of various animal species have been carried out using this method. Besides complementing in some cases the earlier findings of morphology, in others it has helped solve problems in classification that could not be worked out from the morphological evidence at hand, as shown in the work of Boyden and Noble (1933). Serological studies then can be an aid in helping to determine the degree of animal relationships.

### (b). *On the relationships between Cyclostomata, Elasmobranchii and Pisces.*

One very notable result in the attempt to demonstrate relationship between the above classes of Craniata by means of the serological method, was the marked inability of the antisera employed to show any cross reactions between these groups, even with the ring test. When antishark serum, produced by the triple injection method, was reacted with the lamprey (*Petromyzon marinus*) and the sturgeon (*Acipenser rubicundus*), no reaction whatsoever resulted (Table I). The inability to get any reaction between

## ANTIGENS

ANTISERA	Homologous Titer in Millions	ANTIGENS			Ring Tests	Photron'er Tests
		Anti-Shark (S3) (Fo)	Anti-Shark I (Fo)	Anti-Shark II (N)		
Lamprey (Fo)	1.024	0.0	0.0	0.0	0.0	0.0
Shark 39 (Fo)	1.024	100	100	25	100	100
Shark 39 (N)		100	100	100	100	100
Shark 34 (Fo)		50	100	100	94	94
Shark 34 (N)		50	100	100	90.9	90.9
Hypopriion (Fo)		50	50	50	77.9	77.9
Hypopriion (N)		50	50	50	56	56
Scyllium (Fo)		25	12.5	12.5	18.7	18.7
Scyllium (N)		12.5	0.0	0.0	12.9	12.9
Dogfish (Fo)		12.5	0.0	0.0	8.2	8.2
Dogfish (N)					0.0	0.0
B.D. Skate (Fo)	6.25	0.0	0.0	0.0	0.0	0.0
B.D. Skate (N)						
Eagle Ray (Fo)	0.0	0.0	0.0	0.0		
Eagle Ray (N)						
Sturgeon (Fo)	0.0				0.0	0.0

these three classes is an indication of how far apart they really are. These serological differences point to a long evolutionary period during which the serum proteins of these classes have been evolving. The primary object of any classification is to put like things together and to separate the unlike. On this basis, then, there does not seem to be any justification for placing three such widely separated groups, as determined by serological methods, into one class and designating each as a sub-class of the larger group. Measured by our serological "yardstick" the Cyclostomata, Elasmobranchii and Pisces are really distinct classes.

(c.) *On the relationships within the classes of fishes.*

Intra-class variations of serum proteins would not be expected to be as great as between classes. Such intra-class variations do exist, nevertheless, to nearly the same degree as between classes when their serum proteins are compared. As an example, only with antishark serum produced with triple injections was any reaction found between the shark (*Carcharhinus* sp.), the dog-fish (*Squalus acanthias*) and the barn door skate (*Raja laevis*). No reaction whatever with this antishark serum could be shown when tested with the eagle ray (*Aetobatis narinari*) (Table I). The absence of any cross reaction between these two groups indicates relatively distant relationship between these orders of the same class.

Such a result indicates that the sharks and rays have also had a long period of evolutionary divergence. It seems clear then that orders and classes may have very different values as regards their degree of relationship when different vertebrate groups are being discussed. DeFalco (1940) working with birds had no difficulty in showing reactions between the most widely separated orders of this group with serological methods. A further example of the distances which may separate fishes of a group, was the result found with the ganoids, sturgeon (*Acipenser rubicundus*), garpike (*Lepisosteus osseus*) and bowfin (*Amia calva*). The differences here were not as wide, however, as found with the species of Elasmobranchii tested. Triple series antisturgeon serum gave but small reaction with the garpike and bowfin. When a single series antisturgeon serum was tested with these two species, no reaction was recorded, even though with the homologous antigen the potency of the single series antiserum was much greater than that of the antisturgeon produced by the triple series injection.

(d.) *Results which parallel the present classification.\**

In the more closely related groups where antigens were available, the serological

TABLE II.  
Results of Ring Tests in Relation to Titers Homol-Titer = 100%.

## ANTIGENS

ANTISERA	Homol. Titer in Millions	Sturgeon (Fo)	Gar-Pike (Fo)	Bowfin (Fo)	Bowfin (N)	Tarpon (Fo)	Tarpon (N)	Brook Trout (Fo)	Brook Trout (N)	Rainbow Trout (N)	Brown Trout (N)	Carp (Fo)	Carp (N)	Buffalo Fish (N)	Red Horse (N)	Catfish (Fo)	Pike (Fo)	Barracuda (Fo)
Anti-Sturgeon (S3) (Fo)	2.048	100	12.5	1.56		0.0	0.0	0.0				0.0	0.0			0.0	0.0	
Anti-Sturgeon I (Fo)	4.096	100	0.0	0.0		0.0	0.0	0.0				0.0	0.0			0.0	0.0	
Anti-Sturgeon II (Fo)	2.048	100	0.0	0.0		0.0	0.0	0.0				0.0	0.0			0.0	0.0	
Anti-Bowfin I (Fo)	.512	0.0	0.0	100	100	0.0	0.0	0.0				0.0	0.0			0.0	0.0	
Anti-Bowfin II (N)	2.048	0.0	3.12	50	100	0.0	0.0	0.0				0.0	0.0			0.0	0.0	
Anti-Tarpon I (Fo)	1.024		0.0	0.0														
Anti-Tarpon II (Fo)	.032																	
Anti-Brook Trout I (N)	.512				0.0	100	100	100	100	100	50		0.0		3.12	0.0	.20	
Anti-Brook Trout II (N)	.256					0.0	0.0	50	100	50		100	100	6.25	12.5	0.0	0.0	
Anti-Carp (Fo)	.512				.20	0.0	0.0	0.0	0.0			100	100	12.5	12.5	0.0	0.0	
Anti-Carp I (N)	.512				1.56	0.0	0.0	0.0	0.0			100	100	12.5	12.5	0.0	0.0	
Anti-Carp II (N)	.256					0.0	0.0	0.0	0.0			25	100	12.5	12.5	0.0	0.0	

## ANTIGENS

ANTISERA	Homol. Titer in Millions	Bowfin (Fo)	Tarpon (Fo)	Brook Trout (Fo)	Carp (Fo)	Catfish (Fo)	Pike (Fo)	Muskallunge (Fo)	Barracuda (Fo)	Dolphin (Fo)	Black Bass (Fo)	L. M. Bass (Fo)	Rock Bass (Fo)	B.G.S. Fish (Fo)	Perch (Fo)	Pickrel (Fo)	Kingfish (Fo)
Anti-Pike I (Fo)	.512	0.0	0.0	1.56	0.0	3.12	100	25	0.0	.39	0.0	0.0				0.0	0.0
Anti-Pike II (Fo)	.256		0.0	0.0	0.0	.39	100	50	0.0	0.0	0.0	0.0				0.0	0.20
Anti-Muskallunge I (Fo)	.256				0.0	0.0	100	100	0.0	0.0	0.0	0.0			0.0	0.0	0.0
Anti-Muskallunge II (Fo)	.256					0.0	50	100	0.0	0.0	0.0	0.0			0.0	0.0	0.0
Anti-Barracuda I (Fo)	.256				0.0	0.0	0.0	0.0	100	0.0	0.0	0.0			0.0	0.0	0.0
Anti-Barracuda II (Fo)	.512				0.0	0.0	0.0	0.0	.39	0.0	100	50	25	25	6.25	3.12	0.0
Anti-Black Bass I (Fo)	1.024				0.0	0.0	0.0	0.0	1.56	1.56	.78	6.25	1.56	50	6.25	100	0.0
Anti-Black Bass II (Fo)	.512					0.0	0.0	0.0	.39	0.0	100	50	25	25	6.25	100	0.0
Anti-Pickrel I (Fo)	1.024	0.0	0.0	1.56	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.25	1.56	50	6.25	100	0.0
Anti-Pickrel II (Fo)	.512			0.0		0.0	0.0	0.0	0.0	0.0	12.5	12.5	6.25	25	50	100	0.0

TABLE III.

Photron'er Results in Relation to Curve Area Homologous Curve=100%.

## ANTIGENS

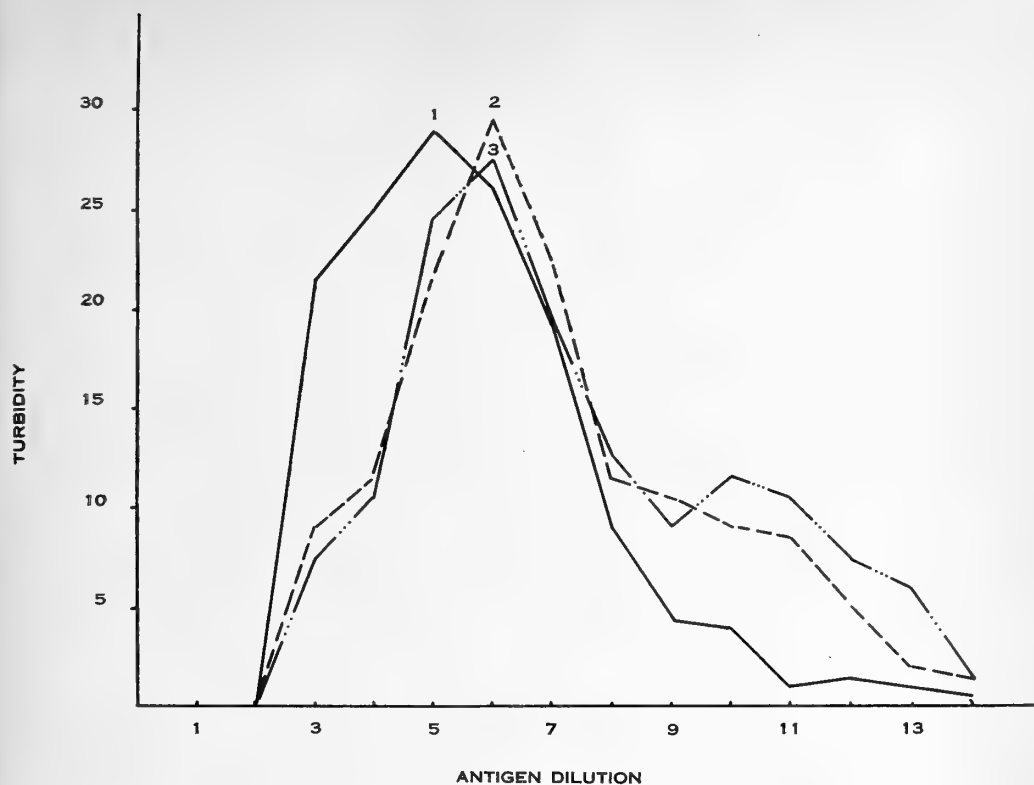
ANTISERA	Shark (39) (Fo)	B.D. Skate (Fo)	Eagle Ray (Fo)	Sturgeon (Fo)	Gar Pike (Fo)	Bowfin (Fo)	Bowfin (N)	Tarpon (Fo)	Tarpon (N)	Brook Trout (Fo)	Brook Trout (N)	Rainbow Trout (N)	Brown Trout (N)	Carp (Fo)	Carp (N)	Buffalo fish (N)	Redhorse (N)	Catfish (Fo)	Pike (Fo)
Anti-Sturgeon (S3) (Fo)	0.0	0.0	0.0	100	4.9	0.0	0.0	0.0	0.0	0.0	0.0	68	60.3	0.0	0.0	6.8	9.3	0.0	0.0
Anti-Sturgeon I (Fo)			0.0	100	0.0	0.0	0.0	0.0				66	53.2	0.0	0.0	0.0	0.0	2.3	0.0
Anti-Sturgeon II (Fo)				100	0.0	0.0	0.0	0.0						0.0	0.0				
Anti-Bowfin (N)				0.0	7.0	63.8	100	0.0		0.0	0.0			0.0	0.0				
Anti-Bowfin (Fo)				0.0	0.0	100	88.6	100		0.0	0.0			0.0	0.0				
Anti-Tarpon I (Fo)						0.0			0.0	0.0	100								
Anti-Tarpon I (N)																			
Anti-Trout I (N)							0.0		0.0	78.6	100				0.0	0.0	0.0	0.0	
Anti-Carp I (N)											100				100	0.0	0.0	0.0	
Anti-Carp II (N)											0.0				100	0.0	0.0	0.0	
Anti-Carp (Fo)														100					

## ANTIGENS

ANTISERA	Brook Trout (Fo)	Carp (Fo)	Catfish (Fo)	Pike (Fo)	Muskallunge (Fo)	Barracuda (Fo)	Black Bass (Fo)	L. M. Bass (Fo)	B.G.S. Fish (Fo)	Rock Bass (Fo)	Perch (Fo)	Pickarel (Fo)
Anti-Pike I (Fo)	0.0	0.0	0.0	100	15.1	0.0						
Anti-Pike II (Fo)			0.0	100	35.6	0.0						
Anti-Muskallunge I (Fo)			0.0	19.1	100	0.0						
Anti-Muskallunge II (Fo)			0.0	20.3	100	0.0						
Anti-Barracuda I (Fo)				0.0		100						
Anti-Black Bass I (Fo)							0.0	45.1	41.2	13.1	0.0	0.0
Anti-Black Bass II (Fo)	0.0						100	74.6	56.8	30.7	4.9	4.6
Anti-Pickarel I (Fo)							100	3.0			12.7	100
Anti-Pickarel II (Fo)	0.0						3.2	11.5		4.0	22.0	100







TEXT-FIG. 1. The comparative values when three different native carp antigens were tested against the same antinative carp serum. Relationships are determined by comparison of total areas of turbidity curves. Although the curves are not identical, the areas of these curves vary less than 2 per cent.

Antiserum	Antigen	Curve	Per Cent.
		No.	Area
Anticarp 2 ×	Carp 1 (N)	1	99.5
	Carp 2 (N)	3	100.0
	Carp 3 (N)	2	98.3

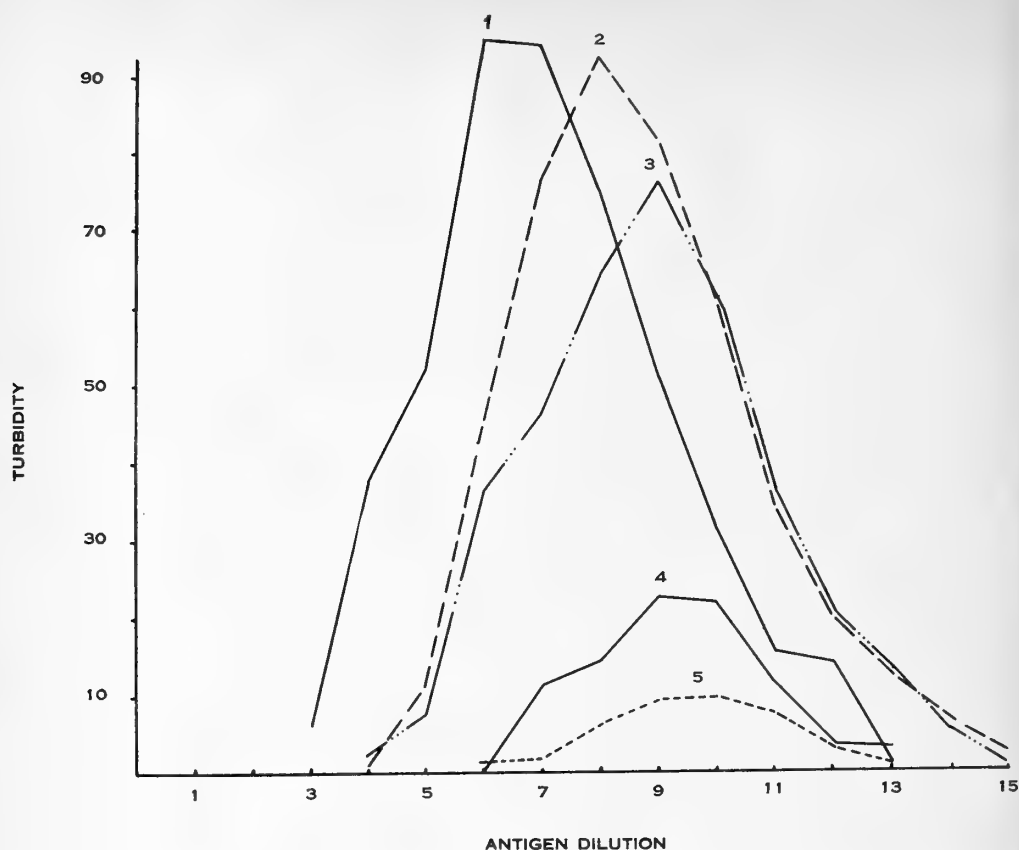
while another showed no reaction with either catfish, carp or trout. The same multiple series catfish antiserum gave a slightly stronger reaction with the pike than it did with two species of marine catfish.

Another result showing an apparent discrepancy with the present systematic position, was the tarpon (*Tarpon atlanticus*) classed as one of the most primitive of the Isopondyli. If any cross reactions with the ganoid antisera could be obtained, the tarpon, as one of the most primitive species of the Teleostei, should show such reaction. No reaction occurred between antibowfin serum and tarpon antigen, nor did antitarpon serum react with bowfin antigen. Table II. These few apparent exceptions to the general parallelism, require confirmation but do not seriously detract from the significance of the results.

#### (f). Possible sources of error in serological studies.

Careful consideration should be given to sources of error that may have a bearing on the analysis of any experimental results obtained. In serological investigations, the effects of lipoids on cross reactions have been studied (Landsteiner, 1936). It has been shown that by the addition of lipoids, cross reactions can be greatly increased. Although lipoids may not be capable of acting as antigens in antibody production, they can combine with serum proteins and act as haptenes and thus decrease the specificity of the reaction.

When the ring test is used in the precipitin reaction for the determination of animal relationships, comparable amounts of antigen and antibody must be used, as only the end point of the reaction is recorded in such



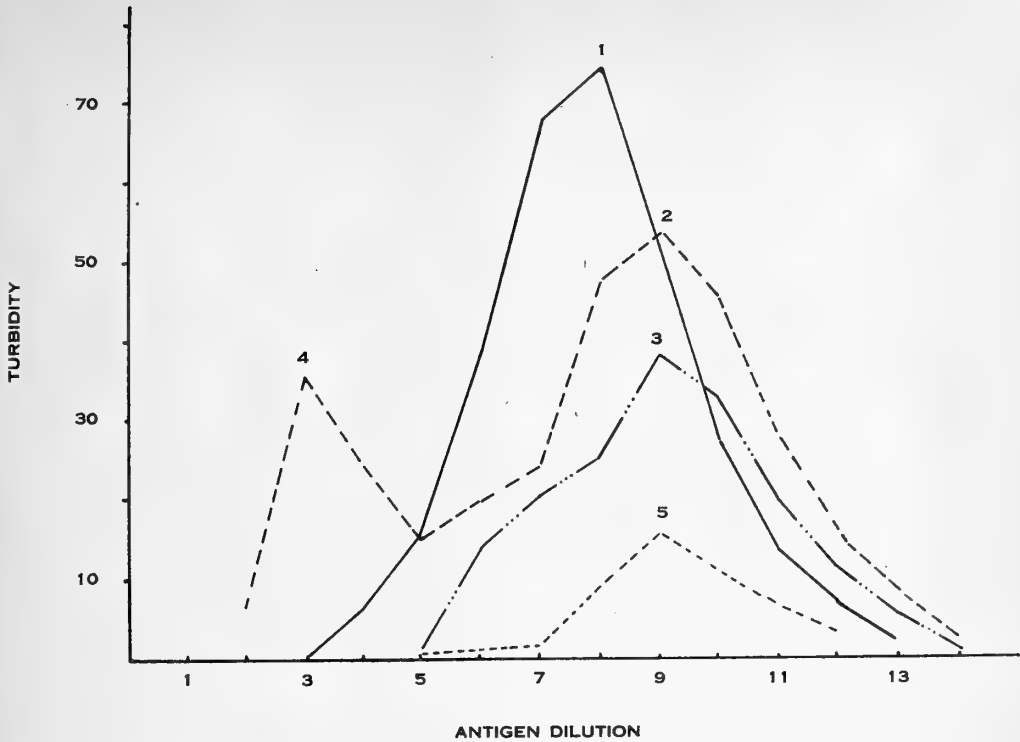
TEXT-FIG. 2. The relationship between different species of Elasmobranchii. This antishark serum was produced by triple injection series of a formolized antigen and only by such means could a reaction be shown with the dogfish. Formolized lamprey, barn door skate and sturgeon did not react with this antiserum.

Antiserum	Antigen	Curve No.	Per Cent. Area
Antishark (S3) (Fo) ×	Shark I (Fo)	1	100.0
	Shark II (Fo)	2	94.1
	Yellow shark (Fo)	3	77.9
	Scyllium (Fo)	4	18.9
	Dogfish (Fo)	5	8.2

determinations. With the photron'er, where the complete range of reaction is represented by the area under the curve, no such procedure is necessary. Where sufficient amounts of antigen and antibody are present, the reaction range is always complete. With constant antibody, the curve area remains the same, for as the amount of the antigen varies, the position only of the curve on the abscissa is changed.

As a rule serum proteins are not homogeneous substances and it is of prime importance to determine, if possible, just what fractions of the serum proteins are most active in antibody production and titration. The amounts and proportions of these pro-

teins may vary in different species and such variation directly affects the antibody produced, which in turn affects the reaction when various antigens are reacted with antiserum. It is especially true that in the ring test, errors may result from comparison of the sera of different species, equivalent in total protein, but different in their content of active protein antigen. On the other hand, in the photron'er comparison with the same sera, no similar errors could occur if complete curves are obtained. In this respect, DeFalco (1940) has made an excellent beginning with the blood serum of birds. He found a wide difference in the albumin globulin ratios of certain birds and



TEXT-FIG. 3. The relationships between the Elasmobranchii with an antishark serum made by a single injection series. The antigen used for anti-serum production was not formalized as with the previous one. Text-figures 2 and 3 show the parallel results obtained with the same species, Text-figure 2 involving only formalized reagents, Text-figure 3, involving only native reagents.

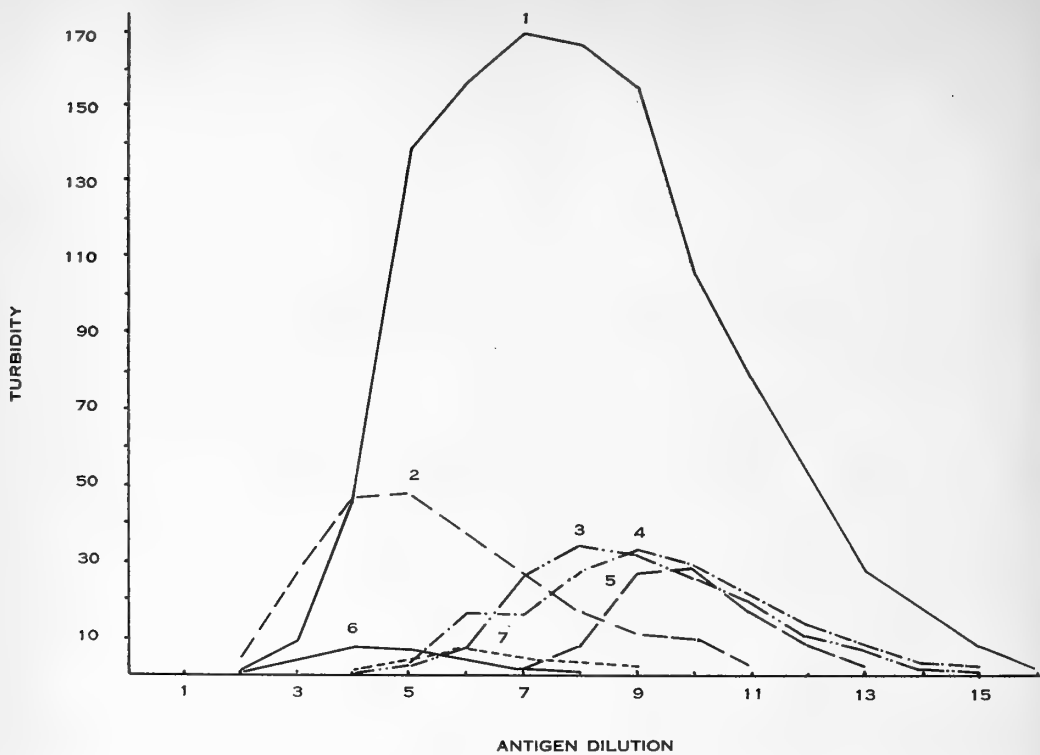
Antiserum	Antigen	Curve Per Cent.	
		No.	Area
Antishark (N2) X	Shark I (N)	1	100.0
	Shark II (N)	2, 4	90.9
	Yellow Shark (N)	3	56.0
	Scyllium (N)	5	12.9

demonstrated that the globulin fraction of blood serum is by far the most active of the proteins in antibody production and titration. Further investigation may show that it is necessary to compare only specific fractions of blood serum and not antigenic mixtures, such as the sera of birds and mammals. It does not necessarily follow that the effects found with birds can be applied to other classes of Craniata, the sera of which may be more nearly constant in their albumin globulin ratios.

If reactions are produced with very distant relatives when a multiple series antiserum with decreased specificity is employed, they should be checked before being accepted. This can be accomplished by dilution of the antiserum. By this means only related species show any cross reactions, thereby eliminating any that may seem doubtful.

(g). General conclusions and problems for future study.

The data presented in this paper seem to justify the conclusion that the precipitin reaction can be of value as a check on the morphological findings in the study of animal relationships. In most cases these findings parallel the systematic position of the several fishes, especially where closely related species are tested. In other cases they show apparent divergence from the usual systematic arrangement. An examination of some of the more recent classifications of fish, constructed entirely from the morphological approach, reveal the wide range in ideas held by taxonomists in general as to what principles should be employed as a foundation for determining the phylogenetic relationship of this rather



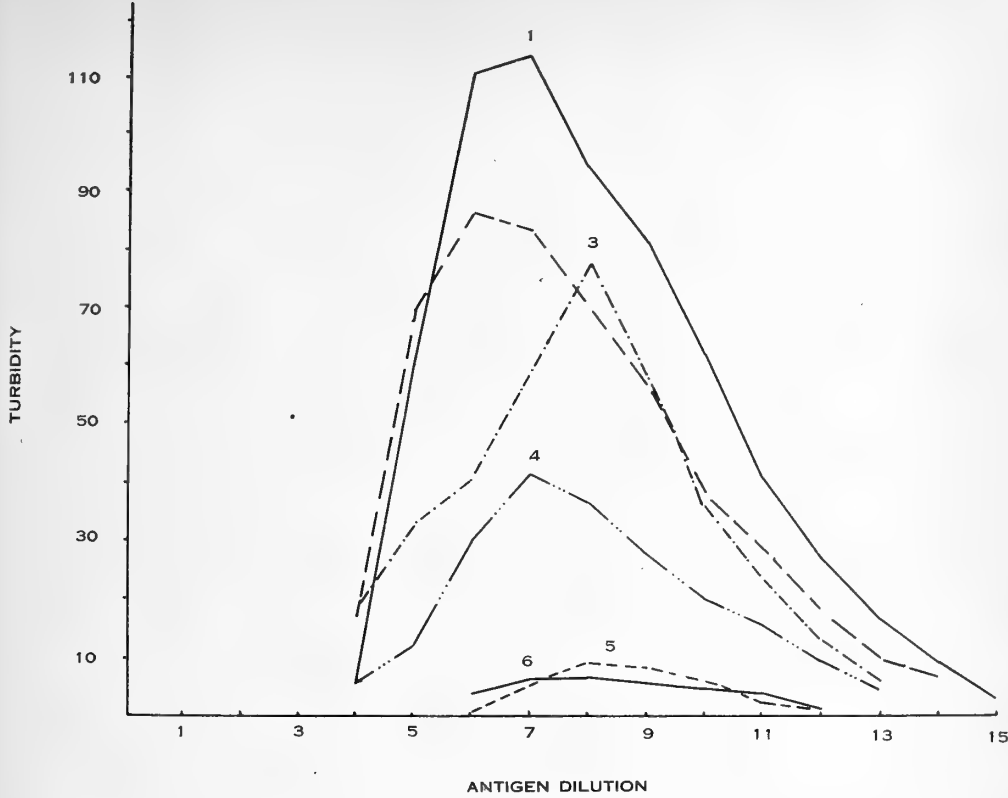
TEXT-FIG. 4. The reaction of antiformolized catfish serum produced by triple series method. The reactions with the formolized antigens indicated here are quite unexpected as enlarged upon in the discussion. Also it may be noted that pike antigen gave a stronger reaction than did either of the marine catfish, and further, the pike cross reaction was stronger than with the carp which is classed in the same order as the catfish. No reactions were produced with formolized barracuda, black bass or sturgeon antigens.

Antiserum	Antigen	Curve No.	Per Cent. Area
Anticatfish (S3) (Fo) ×	Catfish (Fo)	1	100.0
	Pike (Fo)	2	20.2
	Gaff Topsail (Fo)	3	14.7
	Sea Catfish (Fo)	4	15.0
	Bowfin (Fo)	5	7.7
	Carp (Fo)	6	2.0
	Brook Trout (Fo)	7	1.6

highly diversified group. Garstang (1931) states that recent classifications can hardly be taken as an expression of their phylogeny. In any case, a truly natural classification must take into account all the evidence discernable which bears upon the phylogeny. Only by so doing can a classification with probably correct genetic implications result. Because the serological and the morphological methods do not always agree it does not necessarily mean that the one is entirely right and the other entirely wrong. No phylogenetic method is final, be it morphological or serological. In the absence of certain knowledge of phylogeny we are forced to accept the more probable interpretations

of animal relationship and these more probable interpretations must be based on more than one kind of evidence. In a real sense morphology and serology must complement each other.

There is, therefore, a need for further intensive studies among widely separated groups of fish to determine by serological methods what relationships can be shown between orders, families and species. The possible sources of error in the serological method as enumerated in (f) should be thoroughly investigated and their effects noted, so that correct conclusions may be drawn. With more nearly complete knowledge at our disposal, it may be possible to



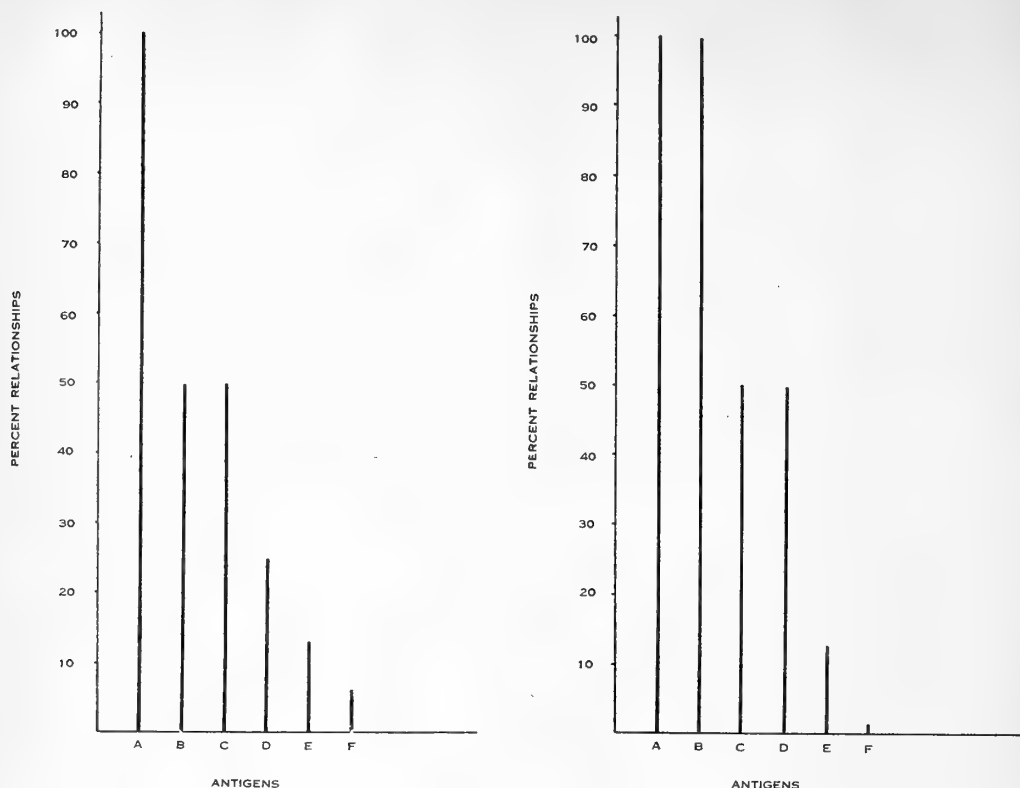
TEXT-FIG. 5. The reaction values between representative species of the group Percoidea. As with the trout species tested the closely related species here are readily differentiated by the photron'er. The representatives of the family Percidae, the perch and the pickerel, seemingly are not closely related to the family Centrarchidae, even though placed in the same group. The black and large mouthed bass, two closely related species, are easily distinguished by the photron'er.

		Curve Per Cent.	
Antiserum	Antigen	No.	Area
Antiblack Bass II (Fo) X	Black Bass (Fo)	1	100.0
	L. M. Bass (Fo)	2	74.6
	B. G. Sunfish (Fo)	3	56.8
	Rock Bass (Fo)	4	30.7
	Perch (Fo)	5	4.9
	Pickerel (Fo)	6	4.6

understand the real significance of the serological methods, especially the precipitin reaction in the determination of the relationships between the different species of fish. It may be that a quantitative basis for the determination of phylogenetic relationships can be established by the precipitin reaction. Such a serological "yardstick," besides its important application in classification, might be of great value in the field of animal breeding and thus mark out new lines of progress in practical genetics.

SUMMARY.

1. The precipitin test has been applied to the comparison of the blood sera of 31 species of fresh and salt water fishes. In all 43 antigens and 26 antisera were used in these tests, which were of two types, the ring test and the photron'er test.
2. Formolized antisera when tested with formolized antigens give parallel values with native antisera tested with native antigens.



TEXT-FIG. 6. The comparative values by the ring test of the Elasmobranchii tested against antiformolized and antinative shark sera. It will be observed that the barn door skate gave a slight reaction when tested against the antiformolized shark serum produced with the triple series method, while none was shown with an antiserum to a single series.

Antishark (S3) (Fo)  
 × A — Shark I (Fo)  
 B — Shark II (Fo)  
 C — Yellow Shark (Fo)  
 D — Scyllium (Fo)  
 E — Dogfish (Fo)  
 F — B. D. Skate (Fo)

Antishark (N2)  
 × A — Shark I (N)  
 B — Shark II (N)  
 C — Yellow Shark (N)  
 D — Shark I (Fo)  
 E — Scyllium (N)  
 F — Dogfish (N)

3. Cyclostomata, Elasmobranchii and Pisces, serologically are sufficiently far apart to be considered distinct classes.
4. Within the Elasmobranchii, antishark serum produced no cross reactions with the rays employed. Only one slight reaction was obtained with the skate.
5. In general the results parallel the taxonomic position based on morphology, but it is clearly evident that the chemical gulf which separates species and orders among fishes is far wider than that in birds.

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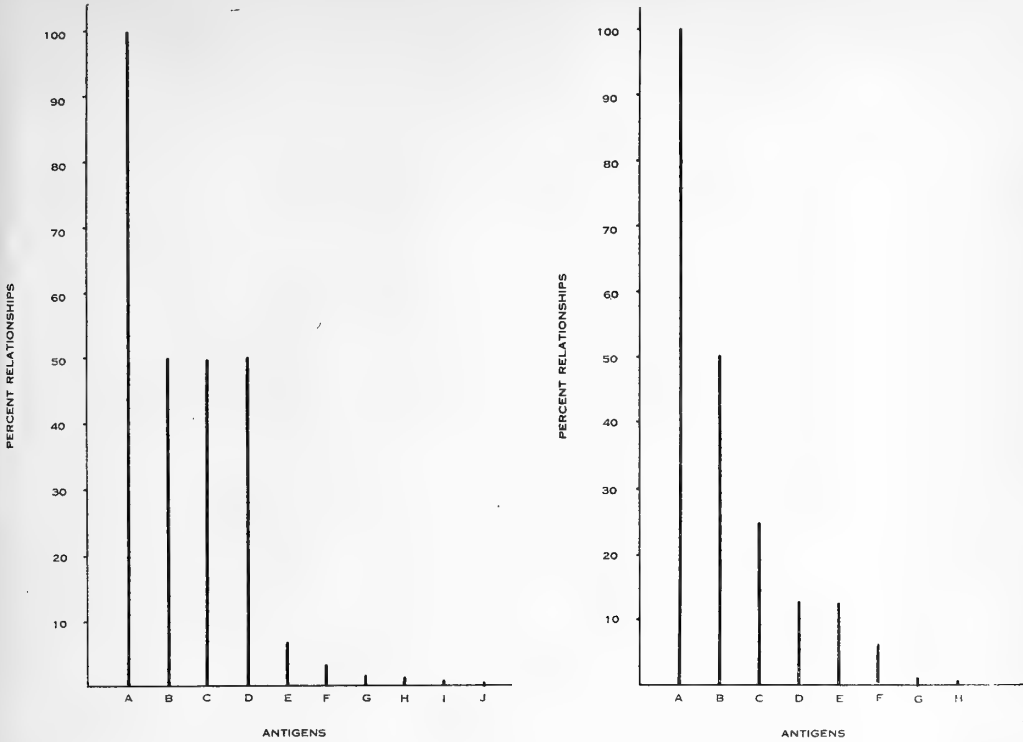
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TEXT-FIG. 7. The reaction values by the ring test when the antiformolized pickrel and black bass antisera were tested with a number of antigens. It will be seen that the ring test brought in more distant relatives than could be shown with these same sera by the photron'er, but in the more closely related species of the Centrarchidae, the differentiation shown with the photron'er was not paralleled by the ring test.

- Antiblack Bass II (Fo)

× A — Black Bass (Fo)  
B — L.M. Bass (Fo)  
C — B.G. Sunfish (Fo)  
D — Rock Bass (Fo)  
E — Perch (Fo)  
F — Pickerel (Fo)  
G — Dolphin (Fo)  
H — Brook Trout (Fo)  
I — Barracuda (Fo)  
J — Kingfish (Fo)
- Antipickrel II (Fo)

× A — Pickerel (Fo)  
B — Perch (Fo)  
C — B.G. Sunfish (Fo)  
D — L.M. Bass (Fo)  
E — Black Bass (Fo)  
F — Rock Bass (Fo)  
G — Barracuda (Fo)  
H — Dolphin (Fo)

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## 16.

Spiders of the Families Lyssomanidae and Salticidae (Magoninae)  
from British Guiana and Venezuela.<sup>1</sup>

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(Text-figures 1-4).

[This contribution is a result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana and to Venezuela, all made under the direction of Dr. William Beebe. The Guiana expeditions were made during the years 1917, 1919, 1920, 1921, 1922 and 1924. The Venezuelan trip, in 1942, was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

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## I. INTRODUCTION.

This is the first of a series of papers on the spiders collected at Kartabo, Bartica District, British Guiana, and Caripito, State of Monagas, Venezuela, by expeditions of the Department of Tropical Research of the New York Zoological Society under the direction of Dr. William Beebe. For maps and ecological data, see Beebe, 1925 and 1943.

The present study is based on the lyssomanids and on the salticids of the subfamily Magoninae in the collection. The 84 specimens comprise 10 species: 3 species (34 individuals) of Lyssomanidae, of which 25

individuals belong to one species, *Lyssomanes nigropictus* Peckham; and 7 species (50 individuals) of Magoninae, of which 25 belong to the new species, *Mago silvae*, there being individually few of the others. Of the 10 species, 8 are regarded as new. Seven were taken in both British Guiana and Venezuela; 2 in British Guiana only and 1 in Venezuela only. In 7 of the species both males and females were taken, and in 4 species enough young, in addition to the adults, to form interesting growth series. Descriptions of colors in life, often so different from those in preservative, habitat notes, and dates of capture of various growth stages are included in most of the species discussed. Further summaries, detailed development studies, and discussion of breeding seasons must await completion of the study of the remaining salticids.

While these data form only a beginning of life history work in these little-known tropical salticids, they furnish an example of the many advantages to be gained by studying tropical animals in the field in one or two adjacent localities throughout a number of seasons. Only by such methods can knowledge of ecological and psychological characters (such as those of display), now recognized as of vital importance even from a purely taxonomic viewpoint, be added to morphological descriptions of species. And only by future comparative studies of all these factors can the evolution and relationships be understood of such an important and puzzling group as the salticids.

In this paper, total length is measured from anterior margin of orbit to posterior tip of abdomen. For convenience, an arbitrary division of young specimens into immature ("imm.") and juvenile ("juv.") stages is made, as follows: A specimen is regarded as immature when the genital organs are well formed, but some obvious weakness of pigmentation, shortness of chelicerae or palp, etc., indicate a pre-adult stage. A

<sup>1</sup> Contribution No. 670, Department of Tropical Research, New York Zoological Society.

spider is listed as juvenile when there is no external development of the bulb on the male palpal tarsus or no visible epigynum in the female.

Petrunkévitch (1911, 1928, 1933) is followed in general classification.

All types are deposited in the collections of the Department of Tropical Research of the New York Zoological Society, Bronx Park, New York City.

My thanks go to Dr. William Beebe for the use of his field notes concerning British Guiana specimens, and to Mr. Henry Fleming, entomologist of the Venezuelan Expedition, for collecting the majority of the Venezuelan specimens. Where not otherwise specified, the field notes are my own.

I wish to express here my appreciation to Dr. Alexander Petrunkevitch and Dr. W. J. Gertsch for their helpfulness with bibliographic questions.

#### FAMILY LYSSOMANIDAE.

##### *Lyssomanes nigropictus* Peckham, 1888.

Text-figs. 1A, B, C, D, E.

*References:* *Lyssomanes nigropictus* Peckham, 1888, p. 235, pl. xi, fig. 10; Simon, 1901, p. 392, figs. 394, 395, 410, 411.

*Color in Life:* Male (Venezuelan specimen): Integument of cephalothorax pale translucent yellow green with median black stripe on thoracic part and another along each side of same, along margin. Anterior eyes translucent yellow green. A black stripe across clypeus, a black spot at base of each chelicera posteriorly, and black bars on inner and outer sides of femur of palpus. All legs paler than cephalothorax, each with black bands on distal end of femur, and on basal and distal ends of tibia; tarsi entirely black; some long black hairs on legs. Abdomen pale translucent yellow green with four pairs of black, irregular-sized spots, those of the most posterior pair being more or less confluent. Preserved specimens agree with Peckham's description: that is, all of the markings remain, but are faded to brown or grayish, while the general color is yellowish to white.

Female (from a painting of a living Guiana specimen, and descriptions of two Venezuelan examples): Like male, except that there are no markings whatever save for the usual black spots in which the dorsal eyes are set; the ocular area is ornamented with a few silvery green (in young) to yellowish (in adult) hairs. A few hairs on legs brownish. Abdomen distinctly richer, darker green than in male.

Immature male (Venezuela): Identical coloring with female, except that reddish-brown is mixed with black on the large tubercle holding the median lateral eyes.

*Remarks:* There seems to be no question

of the identity of the present material from British Guiana and Venezuela with the single "Amazonica" specimen of Peckham (from Simon's collection), both description and figure checking well. The few differences are as follows: the posterior abdominal spots are strongly fused in our specimens, instead of merely "connected by a brown band;" spots at the base of the chelicerae are not mentioned by Peckham, although distinct in all our well developed males; finally, Simon's figure of the chelicera (1901, p. 394, fig. 411) shows only the 4 large teeth, not the additional 3 minute basal ones found in our specimens. In some of our examples these basal teeth are so small and close-set that they could be easily overlooked. Because of the relative abundance of this species, both males and females, in each of the two localities collected, and the identity of non-sexual structures (chelicerae, eyes, etc.), I refer the females listed below to this species without hesitation.

*Measurements in mm.:* Largest male, total length 5.26; cephalothorax 2.46; abdomen 2.8. Smallest male, total length 3.36. Largest female, total length 6.25; cephalothorax 2.25; abdomen 4.0. Smallest female, total length 3.07.

*Range:* Known from "Amazonica;" Kartabo, British Guiana; Caripito, Venezuela.

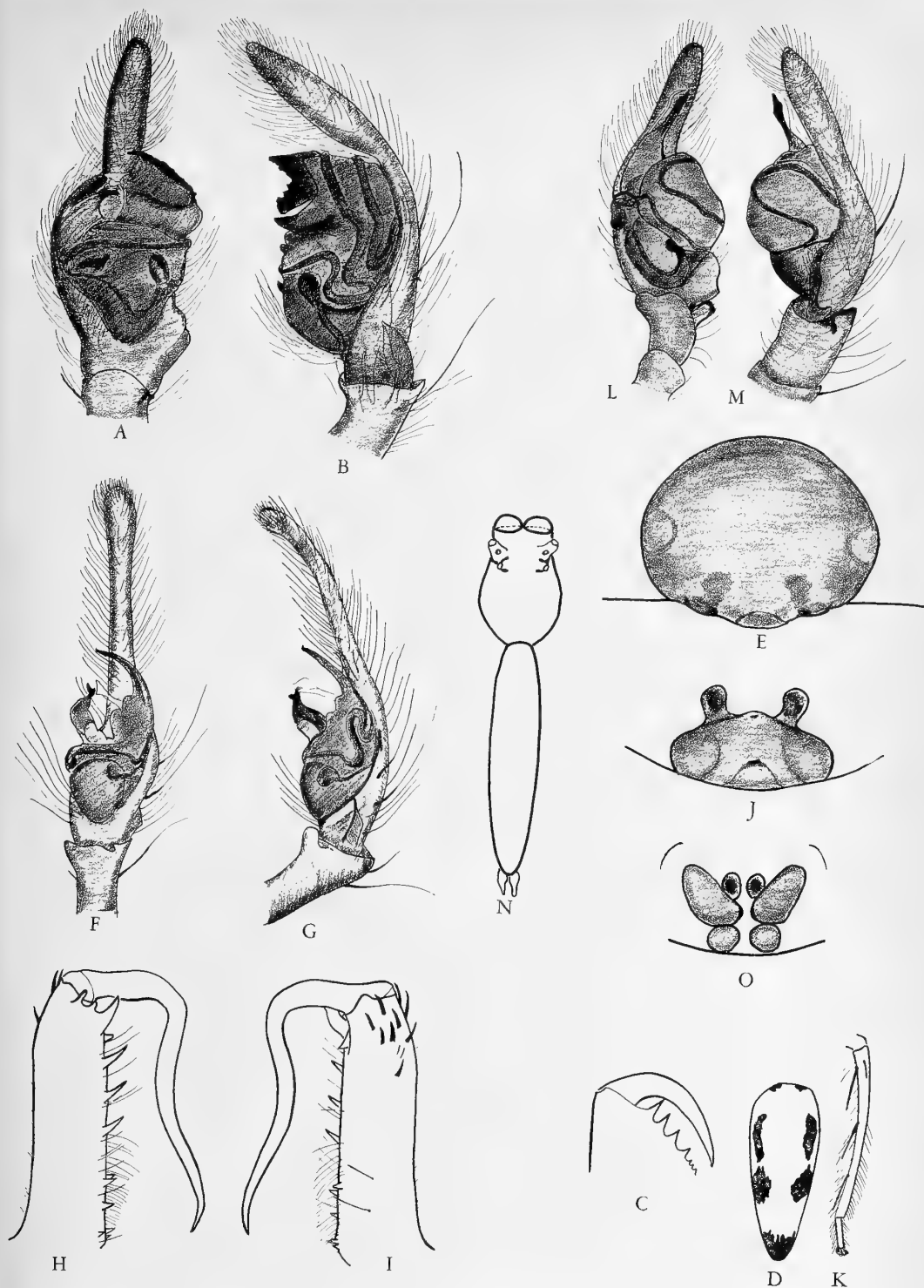
*Local Distribution:* The Caripito specimens were all shaken off bushes and low trees on the edges of sunny jungle roads and along trails through scrub jungle.

*Material:* A total of 25 specimens was taken around Kartabo, Bartica District, British Guiana, and Caripito, State of Monagas, Venezuela, distributed as follows: *Kartabo:* 1917: Sept 2 ♂, 3 ♀, incl. juv. and imm. (Cat. Nos. 1713, 1716, 1733); 1920: June-Dec., 2 ♂, 6 ♀, incl. imm. (Nos. 201619, 201620); 1921: Jan.-April, 1 ♀ (No. 21309); 1922: April 16, 1 ♀ (No. 22216), Feb.-Oct., 1 ♂, 4 ♀, incl. imm. (Nos. 221141, 221142). *Caripito:* 1942: Mar. 11, 1 ♂ (No. 4236); Mar. 22-30, 1 imm. ♀, 1 juv. ♂ (Nos. 42125, 42126); April 1-15, 3 juv. ♀ (No. 42438).

##### *Lyssomanes beebei* sp. nov.

Text-figs. 1F, G, H, I, J, K.

*Color in Life:* Adult male: Unknown. Adult female: "Translucent green, with ocular quadrangle pink" (Beebe). Young female: Cephalothorax translucent night green (Ridgway's Color Key) except for a pair of longitudinal patches of yellow hairs, embracing dorsal eyes and confluent immediately behind anterior eyes; anterior eyes night green; chelicerae, palps, legs and abdomen clear yellow green except for brown fangs and black tarsal tips. Spiderlings, just hatched: "Cephalothorax pale green, abdomen darker green." (Beebe).



TEXT-FIG. 1. **A**, *Lyssomanes nigropictus*, ♂, left palpus, ventral view (drawn with basal part more elevated than in Peckham's view); **B**, same, ectal view; **C**, same, chelicera, ventral view; **D**, same, abdomen, dorsal view; **E**, same, ♀, epigynum (hairs omitted); **F**, *Lyssomanes beebei*, ♂ holotype, left palpus, ventral view; **G**, same, ectal view; **H**, same, chelicera, ventral view; **I**, same, dorsal view; **J**, same, ♀ paratype, epigynum (hairs omitted); **K**, same, ♂ holotype, first metatarsus and tarsus; **L**, *Chinoscopus maculipes*, ♂ holotype, left palpus, ventral view; **M**, same, ectal view; **N**, same, cephalothorax and abdomen, dorsal view; **O**, same, ♀ paratype, epigynum (hairs omitted).

*Color in Alcohol:* Both sexes, as usual, have lost all trace of green, the cephalothorax being yellowish, the abdomen almost white. Dorsal eyes set in two pairs of black spots. Hairs of ocular quadrangle in male scanty, silvery white, in female bright orange, extending down beyond outer margin of anterior eyes, mingled with silvery white ones around and between anterior eyes; in young females the orange hairs are pale yellow. A band of silvery white hairs across clypeus in both sexes. Fang and spines horn-colored. Abdomen of male with a grayish-black marginal band, of irregular width, surrounding it except at extreme posterior tip. No abdominal markings on female.

*Structure:* Male: Cephalic and thoracic parts of cephalothorax about equally long. Eyes of first row twice as large as those of second. Clypeus about two-fifths diameter of anterior eyes. Chelicerae elongate, divergent; 4 teeth on upper margin (2 close together, a third less than half way to tip, and 1 distal); 9 teeth on lower margin (a series of 6, almost equally spaced, increasing in size distally, plus a cluster of 3 unequal ones distally); a group of large, spiny bristles on outer distal end; no teeth on fang. Legs I, II, IV, III. Metatarsus I  $4\frac{1}{2}$  times as long as tarsus; fringes on each side feebly developed, increasing distally. Tibias I and II with 4 pairs of inferior spines and 1 pair of strong laterals, very slightly above and behind distal inferior spines. Metatarsi I and II with 3 pairs beneath. All femora with 1 spine above, near base, 3 beyond middle (1 above, 1 on each side) and 3 near tip (of which 1 or 2 are usually broken off). Palpus as figured.

Female: Thoracic part of cephalothorax relatively longer than in male. Chelicerae well developed but much shorter than in male, scarcely diverging, without distal tooth on upper margin, and with only 7 teeth on the lower, the distal cluster being absent; the outer distal spiny bristles are only feebly represented. Metatarsus I only  $3\frac{1}{2}$  times as long as tarsus; fringes scarcely weaker than in male. Spines exactly as in male. Epigynum as figured.

*Measurements in mm.:* Male holotype, total length 5.47; cephalothorax 2.29; abdomen 3.18; chelicera (excl. fang) 2.46. Female paratype, total length 6.0; cephalothorax 2.36; abdomen 3.64; chelicera (excl. fang) 1.0. Male paratype, imm., total length 5.03. Female, imm., total length 5.81.

*Breeding and Development:* "April 19, 1924: Found female beneath leaf with 20 round, green eggs, deposited singly, close together on a small circular area. Egg .85 mm. in diameter. April 21: Eggs all hatched, or at least ruptured, and gathered in a tiny, white, shrivelled mass at the meeting place

of mouth, leg tips and abdomens of the young spiders. These are in a curious post-ova condition, far from able to move or function. Each large, rounded, green abdomen is bent down, and the legs and palpi all ranged side by side, all centered beneath the cephalothorax. The eyes are very indistinct, merely sketched in, and the whole cephalothorax is swollen, rounded and pale green. The spiderlings are 1.3 mm. long. April 22: The young spiders have unbent, their legs are free and spread out and the mother has devoured all but five of their egg skins, and has spun a little open work tent over the young, so fine that only by holding it against the light is it visible. When disturbed, the young ones scramble around weakly, and the mother creeps over them on guard, and will not leave even when I put the leaf under the microscope." (Beebe).

In the young female, there are only 6 teeth on the lower margin of the chelicera and the epigynum is not developed; the leg spines and general proportions, however, appear quite sufficient for identification.

The chelicerae of the young male are considerably shorter actually and relatively than those of the holotype, but differ in armature only in having the teeth more closely spaced (as in the female) and in having 5 and 7, not 9, large distal bristles on the upper side, on right and left sides respectively. Pigment and palp well developed. The holotype is probably not quite mature, since it appears about to molt.

*Affinities:* The proposed new species seems to be rather closely related to *L. mandibulatus* Cambridge, 1900, from Central America, and to *L. consimilis* Banks, 1929, from Panama. It differs from both, however, in the lack of markings on the thoracic region, in the dentition of the chelicerae, in the spinulation of the legs, and in details of the palp.

*Range:* Known from Kartabo, Bartica District, British Guiana, and Caripito, State of Monagas, Venezuela.

*Material:* A total of 4 specimens (not counting just-hatched spiderlings) was taken as follows: *Kartabo*: 1920: Jan.-April, ♂ holotype (Cat. No. 201621), ♂ paratype, imm. (No. 201622); 1924: April 19, ♀ paratype with spiderlings (No. 24,422). *Caripito*: 1942: Mar. 18, 1 imm. ♀ (No. 4275), shaken from low tree in high jungle.

This species is named in honor of Dr. William Beebe, director of the expeditions.

#### *Chinoscopus maculipes* sp. nov.

Text-figs. 1L, M, N, O.

*Color in Life:* Adult male holotype: Integument of cephalothorax and abdomen entirely translucent lettuce green, except for

a narrow brown stripe extending completely around margins of cephalothorax, including clypeus, and a similar one around abdomen. Dorsal eyes each set in a black base, and these in a single pair of patches of shining white hairs. Palpi and labium reddish-brown. Anterior eyes translucent reddish-brown. Legs translucent and colorless except for purplish-brown bands as follows: on distal end of femur, basal and distal ends of tibia, basal and distal of metatarsus and most of tarsus. In addition, the entire femur and tibia of the front legs especially and second legs somewhat appear bright purple in certain lights; it seems the thread of pigment they contain must be magnified by the curve of the leg, like mercury in a thermometer. Spinnerets reddish-brown.

**Juvenile male:** Differs from adult in being a much yellower green, in lacking the ocular patches of white hairs, and the brown marginal stripes, and in having pigment on the legs only near base and tip of each tibia and base of metatarsus; palpi and spinnerets colorless.

**Color in Alcohol:** In both adult and young described above, as well as in our two remaining male specimens, the integument of cephalothorax and abdomen is yellowish or pale brownish (not dark brown or black as in other males of the genus except *brasiliensis*), and whitish in the young. The white cephalic hairs are largely missing, and have turned yellowish, while the brown stripe is variable in strength, not depending wholly on development. Eyes and spinnerets faded, colorless. The banding of the legs remains, somewhat stronger even than in life, the pigment of femora and tibiae I and II being much stronger in the adult males, darkening the entire segments of the first and much of the second, instead of being confined to thin median threads of pigment.

**Adult females:** Integument of cephalothorax yellowish-white, that of abdomen white. Black bases of dorsal eyes moderately well clothed in yellow hairs. No marginal stripe and no pigment on palpi and spinnerets. Legs white with spots of brown pigment at basal and distal ends of all tibiae, metatarsi and distal parts of tarsus. Fang and epigynum light brown. Labium unpigmented.

**Structure:** Cephalic part of cephalothorax only half as long as thoracic part; ocular quadrangle twice as wide as long; about 5 or 6 very minute teeth on lower margin of chalicera. Palp and epigynum as figured.

**Measurements in mm.:** Male holotype, total length 5.91; carapace 2.04; abdomen 3.83; leg I: femur 4.62, patella .75, tibia 4.35, metatarsus 4.41, tarsus .86. Female paratype, total length 6.02; carapace 1.88; abdomen 4.14; leg I: femur 3.91, patella

.65, tibia 3.48, metatarsus 3.59, tarsus .81. Juv. female, total length 3.38; two juv. males, total lengths 5.5, 6.72.

**Affinities:** In generic characters the proposed new species is a typical *Chinoscopus*. It differs radically from all three forms, *flavus* (Peckham, 1888), *gracilis* (Taczanowski, 1872), *ernsti* (Simon, 1900) and *brasiliensis* Mello-Leitão, 1917, described, however, as follows: The male is light in color in both living and preserved specimens and has a marginal body stripe; black spots or bands are present near the joints of at least the tibiae and metatarsi in all legs in both sexes; details of the palp are distinct; epigynum of the female is quite different from that of *flavens*, the other known female in the genus.

**Range:** Known from Kartabo, Bartica District, British Guiana, and Caripito, State of Monagas, Venezuela.

**Local Distribution:** two males, both adult and young, were shaken at different times from shrubs beside a sunny jungle road.

**Material:** A total of 5 specimens was taken, as follows: *Kartabo*: 1924: April, 1 ♀ paratype (Cat. No. 241010). *Caripito*: 1942: April 3, 1 ♂ holotype (No. 42161); Mar. 22-30, 1 imm. ♂ (No. 42124); May 1-15, 1 imm. ♀ (No. 42439); May 15-30, 1 imm. ♂ (No. 42440).

The name *maculipes* is given this species in reference to the marking on its legs.

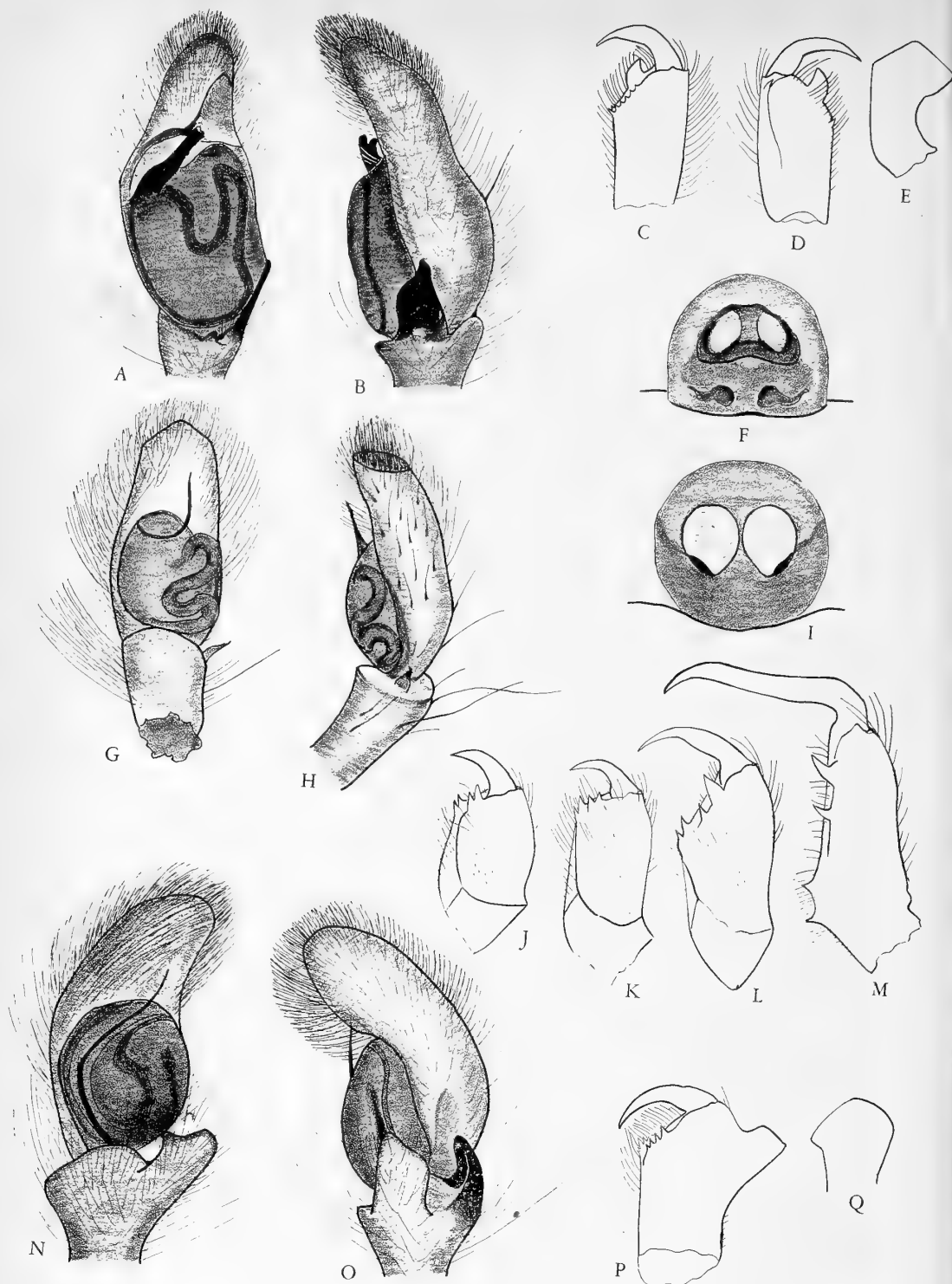
## FAMILY SALTICIDAE.

### Subfamily Magoninae.

#### *Acragas carinatus* sp. nov.

Text-figs. 2A, B, C, D, E, F.

**Color in Alcohol:** Male: Cephalothorax light rufous, paler around margins. Dorsal eyes set in two pairs of black spots; a crest of reddish-orange hairs mixed with black ones behind anterior eyes; a pair of subquadrate patches of white hair between middle and posterior dorsal eyes; a smaller, similar, median patch, often almost rubbed off, behind posterior eyes. All eyes rimmed with reddish-orange hairs; clypeus reddish-brown under eyes, blackish above margin, ornamented medially with a large oval spot of short white hairs. Chelae, mouthparts, tarsus of palp, distal part of all femora and all patellae, tibiae and basal parts of metatarsi chestnut brown. Rest of palp and remaining parts of legs yellowish-white to pale horn. Abdomen above covered with hairs forming a central whitish stripe flanked by two olive stripes, the latter meeting anteriorly, where they are darkened and have a reticulated appearance. Anterior third of abdomen with two well separated pairs, in the olive region, of small, faint, dark, reticulated spots. Posterior third with 2 pairs of strong, black, subquadrate spots,



TEXT-FIG. 2. **A**, *Acragas carinatus*, ♂ paratype, left palpus, ventral view; **B**, same, ectal view; **C**, same, chelicera, ventral view; **D**, same, dorsal view; **E**, same, endite, ventral view (hairs omitted); **F**, same, ♀ paratype, epigynum (hairs omitted); **G**, *Cobanus scintillans*, ♂ holotype, left palpus, ventral view; **H**, same, ectal view; **I**, same, ♀ paratype, epigynum (hairs omitted); **J**, same, chelicera, ventral view; **K**, same, juvenile ♂; **L**, same, immature ♂ paratype; **M**, same, adult ♂ holotype; **N**, *Hypaeus porcatus*, ♂, left palpus, ventral view; **O**, same, ectal view; **P**, same, chelicera, ventral view; **Q**, same, endite (hairs omitted).



and behind them a much fainter third pair. Abdomen below white marginally with entire central portion olive, sometimes faintly striped.

**Female:** Differs from male as follows: The scanty crest is composed entirely of light yellowish hairs; white interocular, postocular and clypeal spots lacking; interocular ones replaced by reddish hairs; abdomen white, unmarked except for a pair of very small, faint spots anteriorly (representing the second faint pair of the male), and posteriorly by the two pairs of strong, black spots; no trace of the fainter third posterior pair of the male. Each of the strong spots is preceded by a small spot of white hairs, better developed before the more posterior pairs of spots.

**Structure:** With the characteristics of the genus. Male chelicera externally with a strong carina ending in a pronounced tooth; upper margin with a large black tooth, compressed, with an oblique inner margin but pointed tip; lower margin with up to 6 minute teeth (5 or less in the immature, and sometimes 6 on one side, 5 on the other); the basal one considerably the largest, decreasing in size distally. External distal part of lamina dilated and subangulate. Palp as figured.

Female differs from male as follows: chelicera smaller, without keel or keel tooth, and with 2 small teeth on upper margin replacing enlarged one of the male. Outer angle of lamina less pronounced. Epigynum as figured.

**Measurements in mm.:** Male holotype, total length 5.88; cephalothorax 2.63; abdomen 3.25. Female paratype, total length 4.72 plus (probably immature; has been partially dried at one time); cephalothorax 2.29; abdomen 2.43. Male paratype, total length 2.63. Two young males, total lengths 4.61 and 5.18. Two juvenile males 4.41 and 3.94.

**Development:** The two juvenile males, in addition to the undifferentiated palp, have the crest rudimentary and entirely red, have female-type chelicera, and lack practically all abdominal pigment except the two pairs of strong black posterior spots, which are as dense as in adults. In one slightly immature male (4.6 mm.), found with the slightly immature female, the dark abdominal stripes are much darker than in any other specimens, almost obliterating the 4 posterior spots. In the other immature male (5.18 mm.) the olive stripes are scarcely developed.

**Affinities:** The proposed new species is closely related to *A. leucaspis* Simon, 1900, and to *A. longimanus* Simon, 1900. According to the descriptions, these three alone have both a cephalic crest and a white cly-

peal spot. The present species differs from the others in the fact that the crest is chiefly red, not entirely black, and in the markings of the abdomen (although all three species share at least two pairs of strong black spots). In addition, it differs from *leucaspis* in the strongly carinated chelicera ending in a distinct tooth, and from *longimanus* in having a maximum of 6, not 5, teeth on the lower margin, and in lacking white spots on the legs.

**Range:** Known from Kartabo. Bartica District, British Guiana, and Caripito, State of Monagas, Venezuela.

**Material:** A total of 7 specimens was taken as follows: *Kartabo*: 1922: Feb.-Oct., 1 ♂ holotype (Cat. No. 221143); 1917: Sept., 1 ♀ paratype (No. 1710), 1 imm. ♂ (No. 1747); 1920: July-Dec., 1 imm. ♂, 2 juv. ♂ (No. 201623). *Caripito*: 1942: June 1-15, 1 ♂ paratype (No. 42441).

The name *carinatus* is given this species in reference to the well developed keel on the male chelicera.

### *Cobanus scintillans* sp. nov.

Text-figs. 2G, H, I, J, K, L, M.

**Color in Life:** Adult male (from holotype): Ocular quadrangle and entire upper portion of abdomen covered with scales of brilliant iridescent metallic green shifting to purple and rosy. Lateral and thoracic parts of cephalothorax as well as clypeus with bright iridescent plum scales. Integument of cephalothorax wood brown, of abdomen paler; under parts not iridescent, sternum brown, abdomen grayish-black. Each of the four anterior eyes surrounded with narrow margin of bright yellow-orange hairs. Legs all unbanded, uniformly pale translucent horn except for anterior pair and femur of second pair, which are covered with scales of bright iridescent plum.

**Immature male (paratype):** Differs from adult in having iridescence on front legs barely developed. Juvenile male: Cephalothorax white except for ocular quadrangle which is brown overlaid with green iridescence shifting to rosy; a median longitudinal white stripe dividing it, which is bounded by an orange russet border running through and slightly below lateral eyes. Abdomen above brown with two longitudinal rows, one on each side of midline, of small white spots, and outside these on each side is a dark stripe. Lateral to these is a pair of white stripes. Ventral side of abdomen brown. Its entire dorsal surface is overlaid lightly with the same green-rosy iridescent scales as are on the ocular quadrangle. Chelicerae, palpi and legs translucent greenish-white; faint iridescence on joints of legs. Large eyes light brown shifting to black, rimmed with white

hairs, except dorsally where they are orangish.

Adult female: Not seen in life. Immature female: exactly like immature male just described. Juvenile female: Cephalothorax buffy yellow; legs greenish; anterior eyes chestnut, rimmed narrowly with white hairs. Abdomen above deeper buff than cephalothorax, sprinkled irregularly with hairs of whitish iridescence and brownish-buff.

*Color in Alcohol:* Males, females and young: Iridescence almost vanished, remaining chiefly around dorsal eyes and, very faintly, on abdomen. Color otherwise as in life, except as follows: Cephalothorax in adults of both sexes reddish-brown, paler in female. Females of all ages with a few rusty hairs around and below dorsal eyes; large eyes framed in white. First legs of male as dark as cephalothorax, with conspicuous black hairs on lower margin of tibia, metatarsus and tarsus; second legs slightly paler; rest pale horn as in life. Legs of female all buffy white. Abdomen of male brownish, unmarked, both above and below; of female buffy white with markings as follows: A pair of longitudinal brown bands of varying width extending throughout most of length, enclosing a median series of 5 or 6 white chevrons; in addition there is a pair of lateral brown stripes; underside with a large central brownish area surrounded by white. In the two youngest males, in preservative, faint subdermal traces of one or two pairs of very faint, dark, blotchy abdominal markings, corresponding to the dark dorsal stripes of the female, are distinguishable. In the youngest females, the cephalothorax is pale brownish, abdomen white, without markings, except subdermal traces as in the males.

*Structure and Affinities:* The proposed new species appears to be closely related to *Cobanus unicolor* Cambridge, 1900, from which it differs in the somewhat less extreme development of the chelicera, lacking a recurved tip and having the 2 pairs of teeth somewhat closer together, even in the largest specimens; also, there is a tooth on the tibial spine of the palp below the hooked tip; similar but more strongly developed pectination is found in *C. erythrocas* Chamberlin & Ivie, 1936. No iridescence is mentioned in the description of *unicolor*, but the scales are so easily dislodged, and their brilliance so weakened by preserving liquid that they could easily have passed unnoticed in *unicolor*. In fact, each of these three characters may prove to be of no separative value, but since the present specimens are the first of the genus taken in South America, *unicolor* being known only from the Costa Rican holotype, it seems wise to refer them to a new species. The Guiana and

Venezuela series are without question identical.

*Measurement in mm.:* Male (holotype), total length 6.05; cephalothorax 2.69; abdomen 3.36; largest female (paratype), total length 5.69; cephalothorax 2.59; abdomen 3.1; immature male (paratype), total length 6.43; immature female (paratype), 5.47; smallest male, 5.38; smallest female, 4.0.

*Development:* The difference in color between adults and young has already been noted. Text-figs. 2J-M inclusive, shows a growth series indicating the development of the chelicerae, which lag behind the palpi and iridescence in development. Note how similar are the chelicerae of the adult female and juvenile male (Text-figs. 2J, 2K), and the fissidentate character of the teeth.

*Range:* Known from Kartabo, Bartica District. British Guiana, and Caripito, State of Monagas, Venezuela.

*Local Distribution:* Three Caripito specimens were shaken off shrubs alongside open jungle roads and from trees in low jungle.

*Material:* A total of 12 specimens was taken as follows: *Kartabo*: 1921: Jan.-April, 1 ♀ (Cat. No. 21311), 1 imm. ♂ (No. 21310); 1922: Feb.-Nov., 1 juv. ♂ (No. 221144). *Caripito*: 1942: Mar. 10, 1 ♂ (holotype) (No. 4232); Mar. 24, 1 imm. ♂ (paratype) (No. 42442); April 1-15, 2 ♀ (paratypes) (No. 42443); Mar. 17, 1 ♂, 1 ♀, both imm. (No. 4267); April 15-30, 1 imm. ♂ (No. 42444); Aug. 1-15, 1 juv. ♂ (No. 42445); Aug. 15, 1 juv. ♀ (No. 42382).

### *Hypaeus porcatus* (Taczanowski).

Text-figs. 2N, O, P, Q.

*References:* *Attus porcatus* Taczanowski, 1871, p. 53, pl. iv, fig. 5.

*Hypaeus porcatus*, Simon, 1900, p. 44; 1901, p. 419, figs. 465, 466.

*Remarks:* A single, slightly immature male was taken at Kartabo, Bartica District, British Guiana, between February and October, 1922, total length 5.95 mm. (Cat. No. 221145). Its youth is shown in the length of the palps, slightly shorter than in Taczanowski's figure, and in the pigmentation of the abdomen, the spots being less distinct than indicated in Simon's description. Otherwise, the specimen agrees perfectly with the latter, except that there are 5, not 4 teeth on the right chelicera, but the typical 4 are found on the left side.

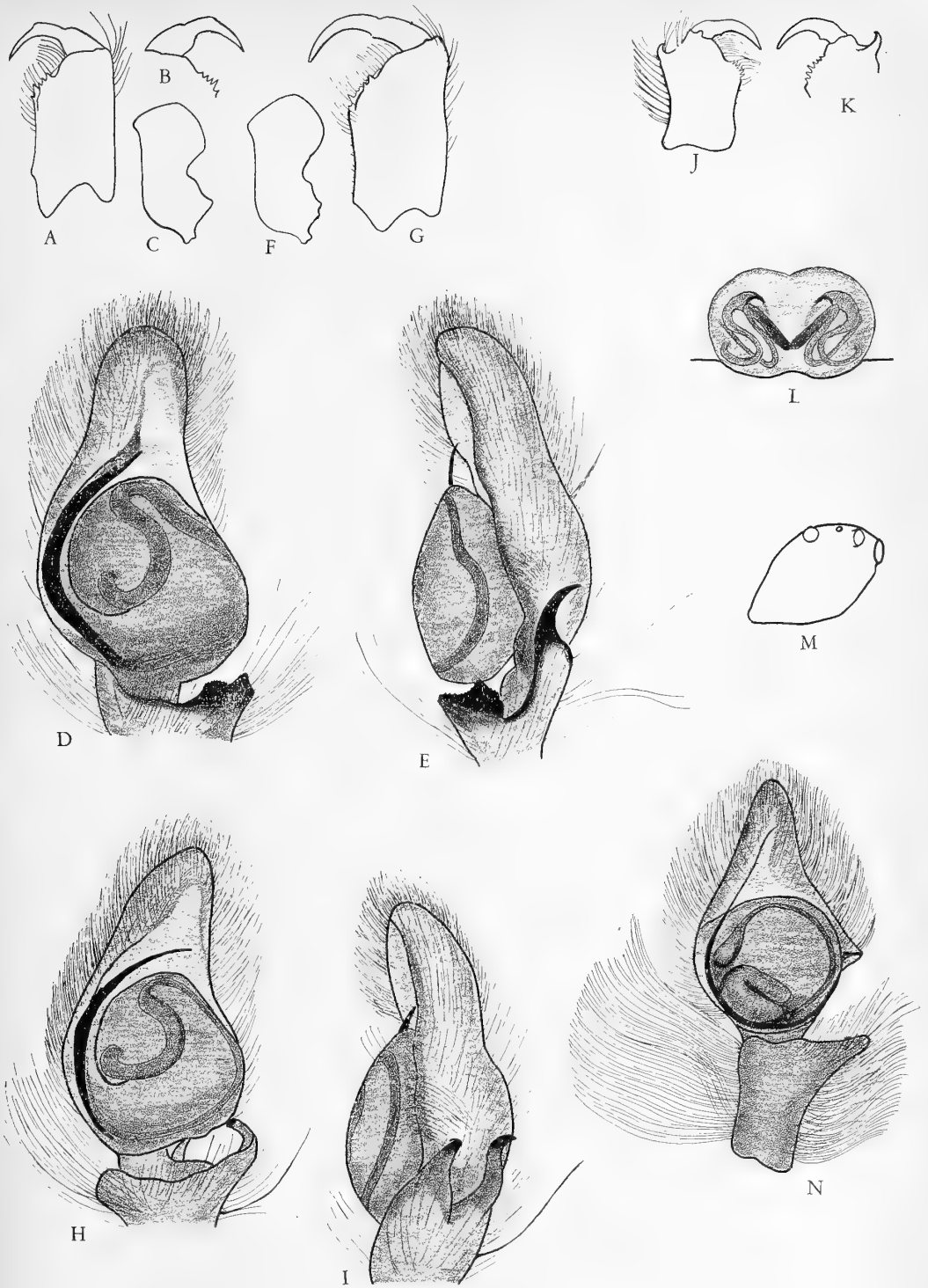
The present specimen extends the known range from French Guiana to British Guiana.

### *Hypaeus flemingi* sp. nov.

Text-figs. 3A, B, C, D, E.

*Color in Life:* Male: Integument of cephalothorax light brown; ocular quadrangle dark brown, with a pair of patches of white





TEXT-FIG. 3. **A**, *Hypaeus flemingi*, ♂ holotype, chelicera, ventral view; **B**, same, dorsal view; **C**, same, endite, ventral view (hairs omitted); **D**, same, left palp, ventral view; **E**, same, ectal view; **F**, *Hypaeus duodentatus*, ♂ holotype, endite, ventral view (hairs omitted); **G**, same, chelicera, ventral view; **H**, same, left palp, ventral view; **I**, same, ectal view; **J**, *Encolpius fimbriatus*, ♂ holotype, right chelicera, ventral view; **K**, same, dorsal view; **L**, same, ♀ paratype, epigynum (hairs omitted); **M**, same, ♂ holotype, cephalothorax, lateral view; **N**, same, left palp, ventral view.

hairs between anterior and posterior dorsal eyes, which are as usual set in black patches. A crest of stiff, short russet and black hairs across ocular quadrangle immediately behind anterior eyes. A prominent patch of white hairs occupying most of clypeus between eyes and chelicerae. Chelicerae and mouthparts chestnut brown. Integument of palp light horny except tibia and tarsus which are dark brown; femur covered with white hairs; two spots of white hairs in front of patella and tibia respectively. First legs entirely dark brown with white spots in front on tip of femur, base of patella and near base of tibia; similar spots present on patella and tibia of second leg; metatarsus and tarsus lighter brown than rest, with a yellowish, translucent area in middle of each. Other legs similar but lighter, and with coxa, trochanter and basal three-fourths of femur translucent light horny; tarsi brownish-black. Abdomen above light olive green with a basal transverse band of dark green, and a broad central greenish-black stripe starting one-quarter of way to tip; this stripe is crossed by two transverse bars of same color, one at its origin, one less than half-way to its end; it broadens irregularly toward the tip, suggesting a third bar. Four pairs of small white spots on abdomen as follows: one spot in front and to outer side of each intersection of a cross bar with the median stripe, and the fourth pair behind. Underside of abdomen pale chartreuse with broad median dark green stripe joining at its base laterally with the broad basal transverse band of dorsal side a pale yellow band just before base of spinnerets.

*Color in Alcohol:* So great has been the change in abdominal markings during the year since the specimen's capture that there is no hint that it is the same spider: the green has completely vanished, as well as all shading, except a trace of the median longitudinal band and three pairs of small, faint spots, the first joined by a very faint cross bar, on the otherwise white abdomen. Underside white, except for two fine, median, subcuticular lines. The cephalothorax and appendages are unchanged, except that in preservative the white spots on palpi and legs are not nearly as conspicuous as in life.

*Structure:* Chelicerae long and slender, without a trace or even a marginal swelling on the outer margin, which is straight. Upper margin of sulcus with 5 small teeth, lower with 3. Endite of pedipalp with outer corner produced, obtuse. Tibia of first leg with 3 pairs of ventral spines and 3 unpaired, anterior, lateral spines, of which the most distal unpaired spine is lower, longer and stronger than the other two. Palp as figured.

*Measurements in mm.:* Total length 5.97 cephalothorax 2.9, abdomen 3.07.

*Affinities:* *H. flemingi* appears to be most closely related to *concinus*, *nigrocomosus* and *cucullatus*, all known only from Simon's type descriptions (1900). In all of these a white clypeal spot is present, a tooth on the outer margin of the chelicera is lacking or reduced to a projection or convexity, and there are only 3 teeth on the lower margin of the sulcus. The present form differs from these in such details as the markings on the abdomen (in both living and preserved specimens), in the whiteness of the interocular spots and, most important, in the described details of the palp.

*Range:* Known only from Caripito, State of Monagas, Venezuela.

*Local Distribution:* Collected by beating shrubs along a sunny jungle road.

*Material:* Caripito: 1942: April 3, 1 ♂ (holotype) (Cat. No. 42155).

This species is named in honor of Mr. Henry Fleming, entomologist of the Venezuelan Expedition, who collected the majority of the spiders.

#### *Hypaeus duodentatus* sp. nov.

Text-figs. 3F, G, H, I.

*Color in Life:* Male: "Cephalothorax terra cotta, with black encircling band. Ocular quadrangle slightly deeper in color, the dorsal eyes set in black, with patches of warm buff hairs between the anterior and posterior dorsal eyes. Chelicerae and mouthparts pompeian red. Palpi warm buff with tarsi brown. Legs warm buff and brown. Cephalothorax below warm buff. Abdomen above warm buff with black markings below, black with buff lateral markings." (Beebe).

*Color in Alcohol:* Markings of legs and upper side of abdomen practically identical with description of these parts in *H. flemingi* in life (p. 000), except that there are only 2, not 4 pairs of white abdominal spots visible (1 pair in front of second cross-bar, 1 pair in front of posterior expansion of median stripe); also, the second cross-bar and the posterior expansion each holds a pair of dark spots; finally, the coloration of these abdominal markings is dull olive brown and buffy white, rather than dark and light green. The "black encircling band" of the cephalothorax mentioned in the field notes of the present species is now only present posteriorly as a narrow marginal line, and anteriorly on the face, on each side of the clypeal patch of white hairs. The rather poorly developed crest is composed chiefly of red hairs with a few black ones in both specimens taken; one of these appears completely mature.

*Structure and affinities:* This species is

very closely related to the preceding, *H. flemingi*, but differs as follows: the chelicerae are shorter and broader, with a slightly sinuous outer margin and with only 2, not 3, teeth on the lower margin of the sulcus; also, the lower spine of the palpal tibia is produced and distally slender, not short and blunt.

*Measurements in mm.*: Male holotype, total length 5.59, cephalothorax 2.69, abdomen 2.9. Male paratype, total length 5.38 (immature).

*Range*: Known only from Kartabo, Bartica District, British Guiana.

*Material*: *Kartabo*: 1922: Feb.-Oct., 1 ♂ (holotype) (Cat. No. 221146). 1924: Mar. 23, 1 ♂ (paratype) (No. 241011).

The species is named in reference to the two teeth on the lower margin of the chelicera.

### *Encolpius fimbriatus* sp. nov.

Text-figs. 3J, K, L, M, N.

*Color in Alcohol*: Male: Integument of cephalothorax reddish-brown (brightest in ocular quadrangle, except for a single pair of elongate black patches in which the dorsal eyes are inserted. A few russet orange hairs of varying length encircling all eyes; a very sparse, irregular sprinkling of minute yellowish white hairs scattered over cephalothorax in general, most numerous immediately behind eyes and on sides of thoracic region; a narrow obsolescent band of white hairs immediately above the dark margins of thoracic region; clypeus with a slightly broader, very dense (but easily destroyed) band of white hairs across its entire margin; clypeus otherwise naked and blackish. Mouthparts and sternum horn-colored. Chelicerae almost black above, brown beneath. Palpi dark brown basally, otherwise pale horn except for brown bulb and spines; all the numerous, long hairs on dorsal and lateral sides pure white. Femur of anterior legs almost black, especially anteriorly; patella and tibia brown, each with a median spot of white hairs in front; metatarsus brown basally and distally, pale horn in the middle; tarsus horn-colored, tips slightly darker. All other legs with femur pale yellowish in basal half, brownish-black distally; the remaining segments very like the corresponding ones of first legs, except that patches of white hairs are rudimentary on the two posterior pairs. Integument of abdomen above light brown with broken transverse dark markings, forming 3 irregular, speckled bands in anterior half, the most posterior being broadest, and 4 similar bands in front of spinnerets, but wavy and much narrower. Entire abdomen with a plentiful covering of short light hairs. Ventral side pale, with patches of dark pigment

laterally, and a large fan-shaped patch around spinnerets.

Female exactly similar to male, even in presence of long white hairs on palpi, except as follows: hairs around eyes are yellowish to whitish, not orange; anterior femora scarcely darkened; other leg segments lighter than in male; abdomen with less pigment, the anterior bands breaking down altogether medially; underside of abdomen with a faint, dark, broad median stripe, and with fan-shaped posterior marking weaker than in male.

*Structure and affinities*: The proposed new species agrees so well with Simon's description of the genus and type species from Brazil (*E. albobarbatus* Simon, 1900, p. 59, and 1901, pp. 421, 427, and fig. 474) that it is possible that adequate series will show them to be identical. The only apparent differences in the males are as follows: In the present specimens there are 6, not 3 or 5, teeth on upper margin of chelicera, and 6, not 4 or 5, in a close-net series on lower margin, on the right side; on the left side, however, in both series the teeth tend to be weak and confluent, some in the upper series being obsolescent; hence, in the genus the teeth number may be quite variable within the species. The remaining differences discernable from the descriptions and single figure consist in the longer tarsus in the palp of the present species, and perhaps a difference in abdominal markings, which Simon has not described in detail. A small, hooked spine on outer, lateral side of tip of palpal tibia in addition to the more anterior elongate process shown in the anterior view figured; bulb rather compressed, little projecting.

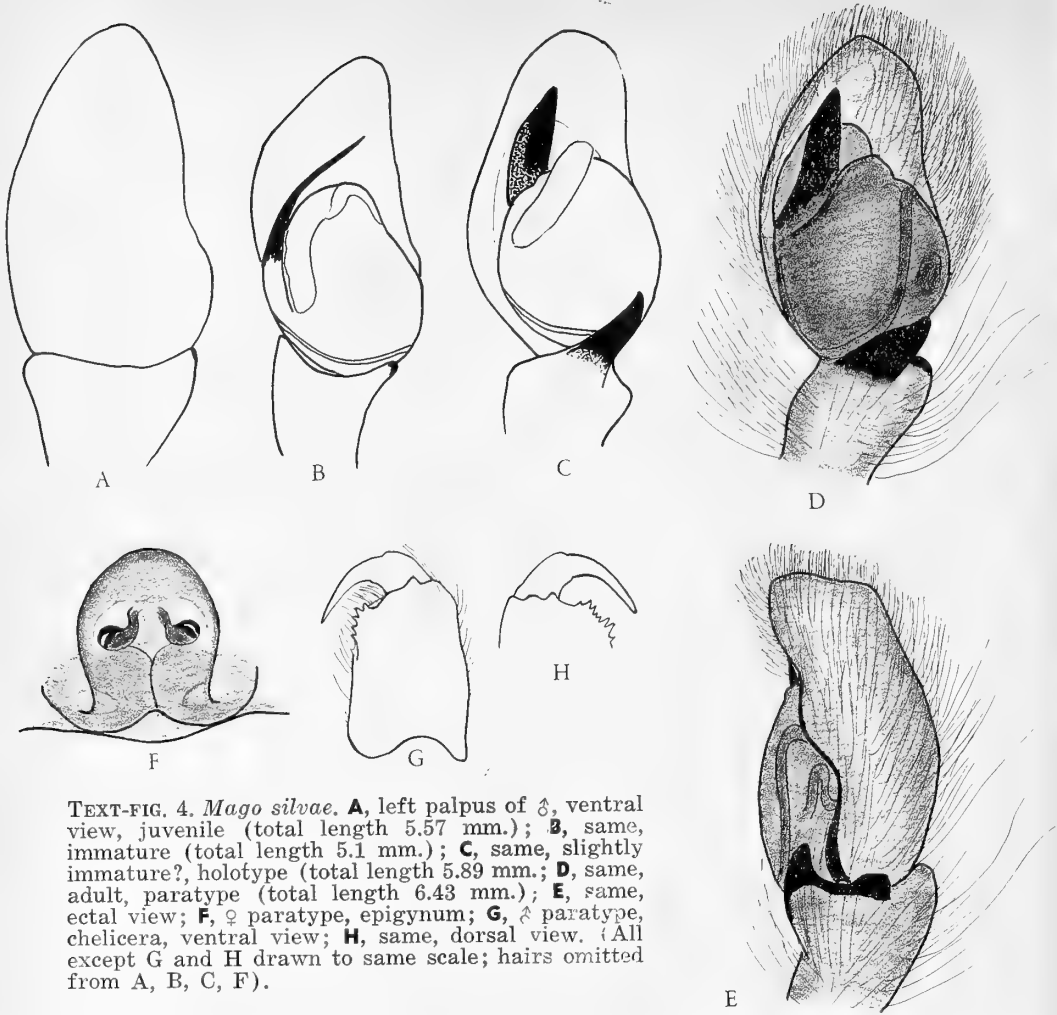
In the female, the median dorsal eyes, although definitely in advance of the middle, are slightly less advanced than in the male. Chelicerae more slender, with 5 teeth on upper margin, 6 on lower, on both sides; no tooth near apex of outer upper margin, but this area is swollen with a distinct summit in the same region which in the male gives rise to the spine. There seems to be no reason to doubt that the two specimens belong to the same species, in spite of the fact that the male is from Kartabo, the smaller, probably immature female, from Caripito.

*Measurements in mm.*: Male, total length 3.97; carapace 2.09; abdomen 1.88. Female, total length 3.49, carapace 1.68, abdomen 1.81.

*Range*: Known from Kartabo, Bartica District, British Guiana, and from Caripito, State of Monagas, Venezuela.

*Material*: *Kartabo*: 1924: April, 1 ♂ (holotype; Cat. No. 241012). *Caripito*: 1942: April 16-30, 1 ♀ (paratype; No. 42446).

The name *fimbriatus* is given this species in reference to the fringed palpi.



TEXT-FIG. 4. *Mago silvae*. **A**, left palp of ♂, ventral view, juvenile (total length 5.57 mm.); **B**, same, immature (total length 5.1 mm.); **C**, same, slightly immature?, holotype (total length 5.89 mm.); **D**, same, adult, paratype (total length 6.43 mm.); **E**, same, ectal view; **F**, ♀ paratype, epigynum; **G**, ♂ paratype, chelicera, ventral view; **H**, same, dorsal view. (All except G and H drawn to same scale; hairs omitted from A, B, C, F).

*Mago silvae* sp. nov.

Text-fig. 4.

**Color in Life:** Adult male: Integument of cephalothorax reddish-brown to brownish-black, the ocular quadrangle and area immediately behind it brightest. Dorsal eyes set in black. Four patches of pale yellow hairs as follows: one on each side between median and posterior dorsal eyes; a small median spot between posterior eyes; a large median spot behind posterior eyes. In addition, there are a few reddish hairs around all dorsal eyes. Large eyes chestnut brown rimmed with yellowish-brown hairs. Chelicerae black; mouthparts tipped with black. Palpi blackish-brown with moderately long, white hairs. First pair of legs considerably darker than others, with two patches of white hairs on anterior central parts of patella and tibia respectively; all legs banded dark and light, the dark ranging from vinaceous brown to dark chestnut, the pale

from buffy pink to light horn, the hairs light or dark corresponding to color of underlying integument. Sternum light brown. Abdomen above tawny olive to blackish-brown, with paler markings, varying from pinkish-buff to white, and poorly to sharply defined. A characteristic general pattern is always discernible, however, including two basal pale cross-bars separated by a dark bar and, behind these, six more or less coalescent and very irregular pale blotches; these are all often overlaid with uneven superficial pigment. Underside of abdomen almost entirely occupied by a dark triangle, vinaceous brown to blackish, traversed medially by a pair of narrow, longitudinal, pale lines, and surrounded laterally and posteriorly in front of spinnerets by gray. (From Beebe notes on Guiana holotype and Crane notes on Venezuelan paratype).

Adult female: Color in life unknown.

Juvenile female: Cephalothorax primuline to ochraceous yellow, naked except for buffy

yellow hairs fringing all eyes. Large eyes ochraceous brown to reddish. Anterior two pairs of legs and their hairs ochraceous orange; remaining legs somewhat paler than cephalothorax; tarsal claws black. Abdomen above and below same shade of yellow as cephalothorax with three pairs of very distinct, dark, dorsal spots and a longitudinal, dark, ventral band, narrower than in adult male. (From Beebe and Crane notes on Guiana and Venezuelan specimens, respectively).

*Color in Alcohol:* Little change, except for the usual fading. Adult female uniformly white except for three pairs of dorsal abdominal spots—larger, paler, and more irregular than in young female—and a dark, ventral, abdominal marking as in adult male. Dorsal abdominal markings in both sexes very variable in both intensity and shape, largely, but not altogether depending on developmental stage. Pattern of male practically identical, under outer epidermis, with that of female. In the male, the median pale hairy spot of ocular quadrangle is stronger in the young than in the adult, while that behind the posterior eyes develops late and is strongest in the adult. Both are easily rubbed off in preserved specimens and may be almost lacking. The paired spots between the dorsal eyes are always much stronger.

*Structure and Affinities:* Judging from Cambridge's (1882) and Simon's (1900, 1901) descriptions, the present species is a typical *Mago*. The character of the cheliceral teeth alone, however, as well as other details, distinguish it from all of Simon's species, while the tibial spines of the palp and the abdominal markings separate it at a glance from Cambridge's *intentus*, in the description of which the dental formula is not given. In the present form there are 7 to 8 (usually 8) unequal teeth on the upper margin, most of them large, except for the fourth, which is minute; 4 to 6 (usually 5) on lower margin; the full complement is not developed until late, well grown females, apparently mature save for incomplete epigyna and more compact abdominal spots, having as few as 2 teeth on lower margin. Unlike the male, the female has no spine on anterior side of first patella, and only one lateral spine (the more distal), on anterior side of first tibia.

The development of the palp is shown in the figures. In only one specimen, the largest (Guiana paratype, No. 1718, shown in the shaded drawing) is the longitudinal tubule on the bulb apparent, or the small loop to the right distinct; also, in all other specimens, the external, smaller, tibial spine is more pointed than in this old specimen. In cheliceral armature, body markings and all

other details, however, this male is typical of the species.

*Measurements in mm.:* Male holotype, total length 5.89, cephalothorax 3.17, abdomen 2.72; largest male (paratype, No. 1718), total length 6.43, cephalothorax 3.36, abdomen 3.07; male paratype (No. 42207), total length 5.38; youngest male, total length 5.57. Largest female (paratype, No. 42447), total length 6.53, cephalothorax 3.36, abdomen 3.17; youngest female (No. 24,111), total length 5.76.

*Range:* Known from Kartabo, Bartica District, British Guiana, and Caripito, State of Monagas, Venezuela.

*Local Distribution:* 9 of the total of 25 specimens taken are known to have been beaten from bushes and low trees on the edge of and within jungle of moderate height.

*Material:* *Kartabo:* 1917 (Sept.): 1 ♂ paratype (Cat No. 1718); 3 ♂ (Nos. 172, 1711, 1743); 1 ♀ paratype (No. 1748); 2 ♀, incl. 1 imm. (No. 1749). 1920 (Nov.): 1 imm. ♂ (No. 201625); 2 imm. ♀ (No. 201624). 1921 (Jan.-April): 1 ♂ (No. 21312). 1922 (Feb.-Oct.): 2 imm. ♂ (No. 221147). 1924 (Feb.-May): 1 ♂ holotype (No. 24182); 3 ♂, 2 ♀, incl. imm. & juv. (Nos. 24111, 241013, 241014). *Caripito:* 1942: April 1-15, 1 ♀ paratype (No. 42447); April 18, 1 ♂ paratype (No. 42207); April 16-30, 2 ♂, incl. juv. (No. 42448); May 23, 1 juv. ♀ (No. 42273); Aug. 15-31, 1 imm. ♂ (No. 42449).

This species is named for its jungle habitat.

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<sup>2</sup> The plates (XI, XII) are missing in most of the  
extant copies of this paper, including the stock now on  
hand at Madison, Wisc. Dr. Petrunkevitch, however, very  
kindly sent me photographs of tracings he made from a  
complete copy some years ago.

# 17.

## Notes on the Breeding of the Empress of Germany's Bird of Paradise in Captivity.

PRINCE K. S. DHARMAKUMARSINHJI OF BHAVNAGAR.

(Plate I).

### Foreword by Jean Delacour.

Birds of Paradise have exerted a strange fascination ever since men have known them. This is not surprising, as their beauty and showiness cannot be surpassed. They have been eagerly sought by aviculturists, as well for public zoological gardens as for private aviaries.

Nearly all the many different species have been obtained from their native haunts in and around New Guinea and kept in Europe, in America, in India and elsewhere. So far, however, none had ever been bred in confinement. Eggs had been laid, and as recently as the last two years the pair of Long-tailed Birds of Paradise in the New York Zoological Park have nested repeatedly, but no further results followed.

Prince Dharmakumarsinhji is the first aviculturist to have met with complete success. A young Empress of Germany's Bird of Paradise has been reared in his aviary. He must be heartily congratulated for such an achievement, more so for having noted so carefully all the observations he has made on this outstanding event.

\* \* \*

On receiving a telegram from Mr. Shaw Mayer, in May, 1939, to the effect that he was passing through Bombay on his way to England with a collection of tropical birds, including many species of Birds of Paradise, I wired to my friend, the Inspector of Aviaries of His Highness the Maharaja Sahib of Bhavnagar, to go to Bombay. I was then at Mussoorie recovering from ill-health; had I been well I could not have resisted seeing this marvellous collection of oriental birds as it passed through India. Within a few days I was informed that the Inspector had bought a pair of *Paradisea apoda augustae-victoriae* and a male of the Lesser Superb Bird of Paradise (*Lophorina superba minor*) and that they were on their way home to Bhavnagar.

On arrival the pair was set free in His Highness' Palace aviary in a suitable cage

facing west, the cage having an interior room higher up if they required more seclusion. The roofing was of tiles with a good 45-degree slope. Below the tiles was wood. Surrounding the aviaries were large trees so that the cages kept cool during the heat of the day. Moreover, the evening sun could only penetrate at a late hour. This environment evidently suited them very well.

In the season during which the birds arrived, they began moulting rapidly, and there was nothing specially interesting except that they slowly became accustomed to the special diet that is given to our Indian birds, which I shall later mention.

The following spring, at the beginning of February, 1940, the male bird showed signs of display and started calling vigorously. The call is a harsh *wauk wauk wauk wauk wauk* continued, as described by different ornithologists concerning the Greater Bird of Paradise. This call is repeated often during the day and is the general call; there are many others that the bird emits. As the hot weather approached, the male was seen displaying. My assistant, the Aviary Inspector in whose charge I had entrusted the birds, mentions that he saw the male displaying as follows: "He lowered his head, drooped his wings and erected his plumes above his back. Sometimes the plumes were not completely erected, however. All this could be seen through the first cage. I had a glimpse of him while he was moving from side to side, hopping on his favorite perch—a horizontal piece of straight wood one inch thick, and three feet long."

I was unfortunately not able to witness the full display as described by my assistant.

Suddenly during the next month, April, 1940, the male commenced shedding his beautiful plumes and to my astonishment they were all discarded within a fortnight. It was then that we noticed that he showed signs of real courting, chasing the female and calling in tones which varied from gurgles to grunts. It was his custom to lower



his head at the same time, emitting short grunts as he approached the female. These gestures appeared to be his true courting. The particular grunt that he emitted then resembled the sound of a motor-bicycle horn. The courting took place in the early hours of the morning and after the new food was put in the cage, which was at 10 A.M., and also during the quiet hours of the afternoon.

During the middle of April the female was seen picking up nesting material. Hence an old crow's nest was put on a branch erected inside the cage. Twelve days later the female had constructed a cup-shaped nest of coconut fibres and new leaf stems inside the crow's nest and we found that she had started incubation of a single egg.

The hen bird was very regular, sitting tighter as the days advanced, leaving the nest two to three times a day and only coming down to feed, refresh herself and preen her feathers.

After the 25th day of incubation the hen bird became very irregular and on the 28th day I could not resist seeing the egg again and examining it. Most unfortunately, the egg was found to be infertile. I now have it in my collection; its measurements are: length, 3.65 cm.; middle 2.65 cm.

During the month of November, 1941, I moved into my own house, Dil-Bahar, where I had special aviaries constructed to suit my birds and where I took over the pair of Birds of Paradise. Here I devoted most of my time to making notes at the commencement of the breeding season. Out of the four cages facing east, the second from the south I selected for the pair. All of the cages were of equal size but the interior was colored differently and there was no extra room as in the palace aviaries. The two middle cages are closed in on three sides with net windows and have a venetian type of window at the back of the wall for ventilation. The front is wire netting with a door for each cage. The cage in which the Birds of Paradise were kept (cage No. 2) is furnished with plants (crotons), dry perches of teak wood laid horizontally, and an old stump of a tree with branches put here and there. A cemented water course passes through all the aviaries to supply fresh running water for drinking and bathing.

The food of the birds has been virtually unchanged since they came into my aviaries. It consists of papaya, bananas and chogo, which latter is a mixture of flour, eggs, meat and ghee made out of butter. Live food is also given, including grasshoppers, mole-crickets and locusts. I find that the birds relish this mixed diet and thrive on it. The breeding of my pair would indicate an adequate diet.

Throughout the winter months the male

was calling, although not as vigorously as in February and March. The diversity of calls that he emitted was extraordinary, varying in strength in different degrees and rather difficult to describe. Nevertheless I was able to notice that the male had definitely a peculiar call during the real courtship or rather during the height of love-making. This call was a short syllabled, horn-like sound as mentioned before. There was also another peculiar call that seemed similar to that of our Indian tree-pie; this also was heard only during the breeding season. The former love call is generally emitted at the approach of the female or when close to her. Moreover, it was the male's daily habit to bow his head from side to side, then suddenly jerking it up like a mallard drake and shaking it in pride.

During the entire month of March, the male bird was calling incessantly throughout the day but no special display was to be seen except at the end of the month when he was heard emitting his peculiar courtship grunts. At this time both birds were very shy, especially the female which had a very acute sense of danger and vigilant eyesight. The latter was indicated when I was in the habit of looking from the adjoining aviary (No. 3) to see if I could catch the male displaying or luckily happen to see them mating. In order to do so I had drilled two small holes through the cement sheeting on the sides of the aviary. The two holes were three feet apart and the size of a 22 calibre rifle bullet hole. From here I could observe from time to time the male coming down to feed, taking his daily bath in the early morning and dancing about on the branches. After taking his dip he would dry himself on his perch, preening his beautiful plumes. The hen bird would also bathe but not so regularly as the male. This may have been because she could perceive me through that minute hole and catch any slight movement that I made. She was very wary and became more suspicious toward the direction of the holes. However, it does not seem unusual among these birds to be suspicious, for in the dense jungles of New Guinea there must be many of their enemies lurking close by. Moreover, they are birds that normally prefer absolute seclusion among dense foliage.

While the male had his own courtship and display, I noticed also that the female seemed very active. She would exercise in a peculiar manner which coincided with the display of the male. She would leave her perch, fly toward the open side of the cage and make one or two short circles and return. At first I imagined this to be merely the usual exercise. But making further observations I noticed that it was a part of the pro-breeding display, if one may call



it so. She would sometime fly around the male in this manner, too. This latter behavior overcame my doubt.

The female Bird of Paradise had a habit of moving from one side to the other on a branch, often turning completely round and flipping her wings as do crows. This behavior of wheeling, as I might call it, is also to be seen among babblers. They are very cautious birds and do not alight on the ground if they can help it. This characteristic is so pronounced that they will climb down a branch, lower the head, take a drink, go up again and fly to their perch. When coming down to feed they will fly to a slender branch of a bush, alighting invariably in a horizontal fashion. Then they wheel about as they climb down with one foot above the other, see that there is no danger, and then come down to feed. I have seen the female scale an old trunk of a tree not unlike a woodpecker looking into the crannies for insects.

During April, although the climate became a little warmer as the southeast winds began to blow, there was a cool breeze coming from over the sea. This seemed to stimulate the birds immensely. The male started his displays. Hopping on his branch, with both feet simultaneously, he would jump up one or two inches, as it seemed; in springing himself up he would also move his wings rapidly. Then he would fly to another branch, do the same and return. He would also hop from side to side on his favorite perch, lowering his head from one side to the other and making his courtship grunts. This kind of display lasted fifteen days from April 5 to April 20. During the second week of April, after the 17th, the hen bird was for the first time seen picking up a stem of lucerne in her beak and carrying it towards nest No. 2, an old crow's nest composed of bits of wire, which had been placed in the northeast corner of the aviary about a month before.

This was the first sign of nest building. The southeast winds continued.

On April 21 the male was not calling as much as usual. The next day I arranged to put creepers, lucerne and fibers for nesting material into the aviary. New material was given each day but the female preferred the lucerne, flying to nest No. 2 and depositing the succulent stems untidily. Many of them dropped out of the nest, while some were not even properly arranged. The building procedure continued every day but only in the morning hours between 9 and 10:30 o'clock. Some creepers fell down each day while new ones were roughly put on the nest. As the days advanced only a few remained on the nest. This type of haphazard nest building went on until April 27 when everything ceased and there were no signs of picking up of material. By this time only

a few stems of lucerne, that had fixed themselves in the wire nest, remained. Whether the hen bird had become suspicious or whether she was bluffing was a question to be answered later. However, I kept a close watch and found that the male bird was again calling vigorously and was seen chasing the female.

On May 6 I was spraying water with my hose pipe into the cages because of the tremendous heat. It was my habit to spray the casuarina branches that screened part of the south and west walls at the back of the aviary. I did not notice the hen bird move as she regularly did from behind the screen. However, a few minutes later when I had stopped spraying, she flew out of the casuarinas and she perched on a branch in the front part of the cage. She immediately started drying herself, and having done so at once flew back to her usual resting place. In spite of this new observation, which I then took to be quite natural, I passed the cage to water the others.

Two days later, on May 8, my aviary boy reported the nest and a single egg of the Paradise Birds among the casuarina branches. His suspicion had been aroused because the hen bird was not to be seen in the cage and on investigating in the casuarina screen, he eventually flushed the bird off the nest. I confirmed his statement by seeing the egg by means of a small mirror fastened to a cane stick. The nest was a regular cup shape and was placed between the stems of the thickest clump of branches. It was quite invisible from outside. A glimpse of the hen bird could be seen from the adjoining aviary but only if the place were pointed out to one. Such was the cunning of the female which had ingeniously avoided our attentions and had surreptitiously built her nest. From May 8 I took particular care and put down my notes.

The hen bird would come down from the nest to feed and clean herself three or four times a day and would remain out from five to ten minutes on each occasion. The male kept fairly silent and never interfered, only making his grunts and gurgles when the hen left her nest. I could generally tell when the female had left the nest by the male making his love calls. On May 17 and 18 the hen was very hard set. On May 20 one of my female dayal birds got into the cage and caused a little trouble before I could remove her. Actually I opened the first cage window so that she could return but I found by doing so a pair of spreo starlings entered the cage, too. However, I managed to entice them out except for a spreo which was so obstinate as not to leave the cage.

The next day, May 21, at 2 P.M., I found near the front of the cage an empty egg shell which I at once recognized as that of

the Bird of Paradise. The first thought that gripped me was that the spreo starling had done the mischief, for often they have swallowed and destroyed the eggs of other birds. The next instant I was in the cage with my mirror to examine the nest and to my delight I saw a little chick, an absolutely pink little thing lying on its side. At once I had the spreo removed. Counting the days from May 8, the incubation period evidently was 13 days, but I am inclined to think that the egg was laid earlier—probably on May 6, so that the incubation period would be 15 days. However, this is a point to be confirmed when better chances afford.

The hen brooded the chick most of the time and started feeding it, as I noticed, at midday. The feeding procedure was extremely interesting. Grasshoppers were put down. She would select one, 1 or 2 inches long, take it to a near branch, then fix it in her claws and start removing its legs, then its wings, and finally would swallow it whole. Seeing that there was no danger, she would fly to the nest and regurgitate the food into the mouth of the young.

After four days the hen bird would take two grasshoppers at a time and regurgitate them both into the mouth of the nestling, one by one. During the next week large grasshoppers were given as well as locusts. These the hen apparently preferred to the smaller ones. In this case also she would take a locust or large grasshopper and proceed with it in the usual manner, removing the legs and wings and also the intestines. The latter were cleverly removed. Then piece by piece she would swallow the soft abdomen and lastly the head, which evidently was an edible portion of the body. However, there was one special peculiarity that I marked about the parent bird during the feeding; that was that she fed the young only twice at each feeding time. This seemed to me very strange. However, when the nestling was 10 days old she would take two or three small grasshoppers and swallow them entire at a time, and would regurgitate them out one by one. She would only bother herself to remove the legs and wings in the case of larger insects. After each feeding the hen picked up the excreta of the chick, which she swallowed in the manner of many other birds during their parental care.

During the first week, I started with only three feedings, one at 9 A.M., the second at noon and the third at 4 P.M. During the second week I increased the feedings to five, at 7:30 and 11 A.M., 2, 4 and 6 P.M. and continued the same until the young left the nest. The number of insects varied at each feeding. When large insects were given the number was usually small—thus, five or six large insects or as many as twenty small ones.

The voice of the chick could be heard at a distance of 10 feet when it was one week old and at 15 days the chattering was audible at 30 feet.

The temperature in the shade of June 3 registered 110 F. This was at the hottest part of the day. The heat was intense, especially on the roof and inside, despite two layers of cement sheeting with a one-inch air space. On Friday June 5, there was a distressing scene, the nestling falling to the ground. Fortunately it escaped injury. Why it should have fallen seemed a mystery, but I later concluded that it was a result of activity induced by the extreme heat and the lack of ventilation near the nest.

At the end of the first fortnight the tender wing feathers were clearly visible, the pectorals were merely hairs, and the tail feathers were starting to grow. The nestling was handled with care and was returned to the nest. It croaked once or twice while on the hand. The legs were still colorless and white. The iris of the eye was lead gray. During this period of intense heat the nestling fell out of the nest again, but since there was straw on the ground, it did not sustain injury and was returned to the nest.

On June 8, 10 and 12 I took photographs of the parent bird feeding the nestling.

After June 10 the temperature dropped and it varied from 105 to 107 degrees F.

The male bird took no part in parental care, but on the contrary became quite a nuisance at times. In fact, he seemed rather henpecked. The female would fly at him and claw him if he ventured too near the nest. The male became sluggish, and would sit placidly in his usual perch in the corner opposite the nest. He was removed as the young got older, as a safety measure.

To give a more detailed description of the nest, it was cup-shaped and measured  $4\frac{1}{4}$  inches wide and  $3\frac{1}{2}$  inches deep. It was composed mostly of causerina leaves and creepers of *Jacaramontsia*, which has a beautiful blue flower. There were, however, a few coconut fibres. The height from the ground was 7 ft. 4 in. and the nest was situated in the southwest corner of the cage.

On June 21 the nestling was able to fly out of the nest. It was fully fledged and looked very much like its mother except that the nape was not so lightly colored as in the parent bird. The eyes were different and the legs lighter in color. It would fly behind its mother for food, and slowly started to feed on its own.

During the entire period of parental care the hen bird emitted a call that I had not previously noted. It was an alarm call, sounding like *Kurr Kurr Kurr*, resembling the call of some of the larger woodpeckers. This call was only heard during the period of parental care and was quite different from the call the female ordinarily emitted.

Her call does not vary as much as that of the male, but is shriller.

[On April 28, 1943, Prince Dharmakumarsinhji wrote Dr. A. Wetmore, of the Smithsonian Institution, as follows]:

"My adult male *Paradisea apoda augustae* suddenly died on February 17, although a week before he was seen courting and I had every hope that the pair would breed successfully again.

"I had been surprised when my cage boy reported that the adult hen was showing signs of nest building. This was on March 7. The situation of the nest this time was in the adjacent corner or N. W. direction of the aviary among the casuarina branches. I promptly inspected the place and could not ascertain it as a nest, although I had seen the hen bird sitting there quite often and breaking leaves. Ten days later nest building commenced in the usual slow manner on a dried bush of a *Duranta* situated in the

front part of the aviary. Creepers with their blue flowers hanging on their stems were placed on the bush each day until active nest building took place on March 20 and 21 and a complete cup-shaped nest was built. Moreover, on March 22 the hen started incubating a single egg. The nest was composed of creeper and pieces of coconut fibre with a bit of string and was lined inside with casuarina leaves. The height from the ground was 3 feet 7 inches.

"Incubation was very regular. She would not stir even when the cage boy went in regularly to clean the cage and put down the food. On April 14 I took the egg, which I believe was addled, while it was still being incubated most regularly. For the next few days the adult hen bird could be seen perched on the nest with a mournful air. After that she began destroying the nest completely. Let me hope that the young bird of her previous nesting will turn out to be a male."

## EXPLANATION OF THE PLATE.

## PLATE I.

Fig. 1. Female Empress of Germany's Bird of  
Paradise on her nest in the aviary.

Fig. 2. Female feeding the nestling.

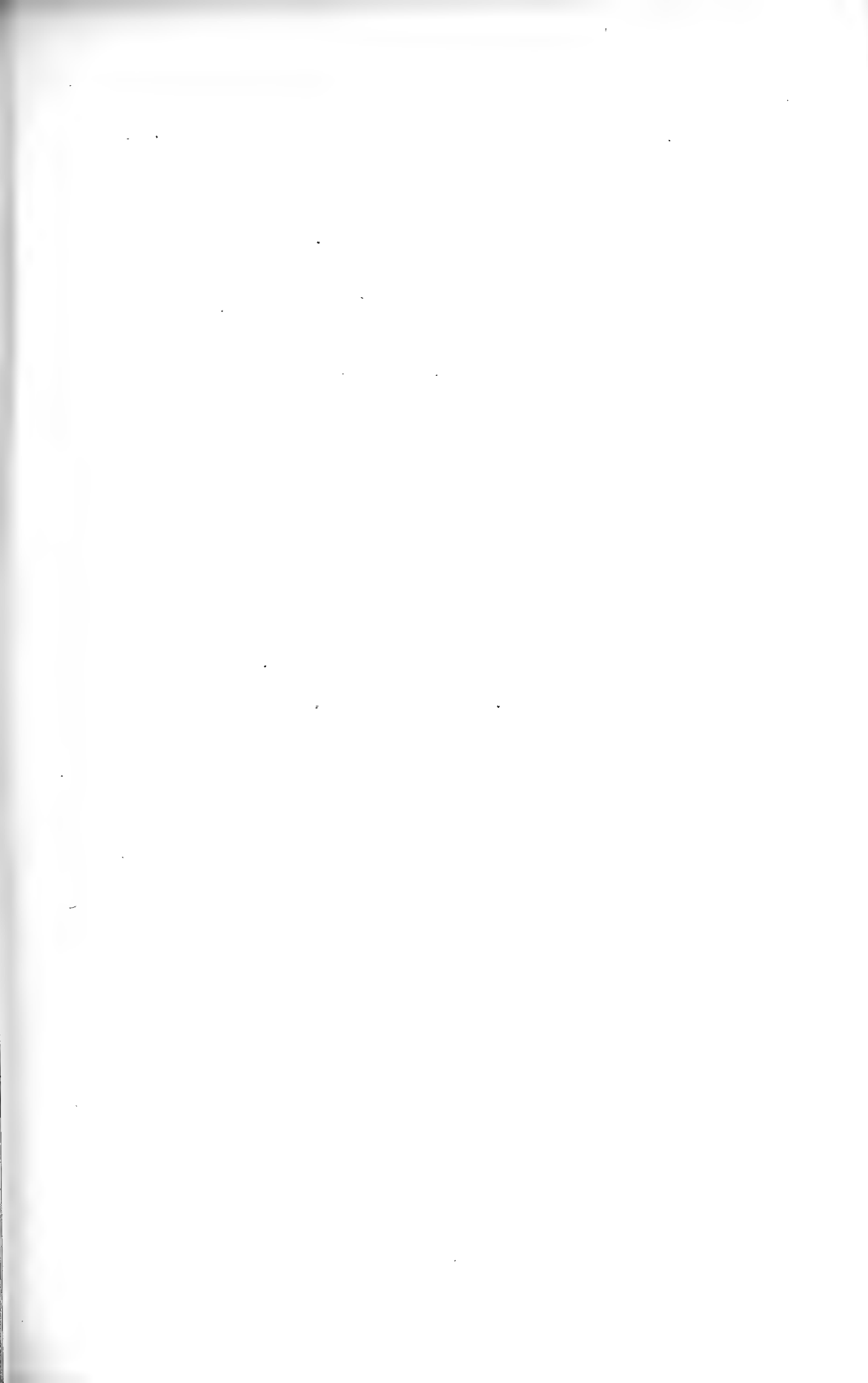




FIG. 1.



FIG. 2.

NOTES ON THE BREEDING OF THE EMPRESS OF GERMANY'S BIRD OF PARADISE IN CAPTIVITY.

## 18.

## Evidence of Healed Hungerosteomalacia (Late Rickets) in a Green Monkey (*Cercopithecus sabaeus*).

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(Plate I).

Deformities of the skeleton in domestic and captive animals, particularly in monkeys, have been repeatedly reported in the literature. The value of many of the earlier reports, however, is limited to the mere recording of the deformation. The pathogenesis of the skeletal changes is often omitted or dealt with rather incompletely, as in the accounts of Bland Sutton (1888) and Dräseke (1906) who diagnosed all deformities found in monkeys, lions, bears, birds and dogs as rickets, although some of their cases had undoubtedly nothing to do with vitamin D deficiency.

The confusion in the pathology of bone in animals was largely cleared up by Christeller (1923) who definitely distinguished rickets and *ostitis fibrosa v. Recklinghausen* in a considerable number of his monkey cases. However, Christeller has not sufficiently separated *ostitis fibrosa* from *osteitis deformans* (Paget's disease), probably because these diseases were at that time not recognized as two entirely different conditions. After the comprehensive study of Christeller who had based his diagnosis on careful macroscopical, histological and radiological examination, only a few well studied cases of bone softening in animals have been recorded. Osteomalacia in cattle was clinically observed by Meador (1927) and McIntosh (1928), in a racing pony by Hewlett (1927) and in swine by Kinsley (1928) and Bouchet (1931). Rickets in carnivores was observed by Maignon (1931) and late rickets in a fossil bear by Jarisch (1937).

Since in the present case a fairly complete clinical, post mortem and laboratory examination could be carried out, a brief record of these findings may be a useful contribution to the knowledge of bone pathology in captive animals, and a help to the veterinarian in evaluating his cases.

### CASE REPORT.

#### History.

A female green monkey (*Cercopithecus sabaeus*), about three years old, which had been fed on a diet consisting only of milk and bread, was given to the Zoological Park, Bronx Park, New York City, because it had bitten its owner. A deformity of the right thigh was detected, but otherwise the monkey seemed normal. The animal was transferred to the Department of Anatomy, New York University College of Medicine, for further study. After radiological studies and chemical examination of the blood had been made, the monkey was killed with chloroform and the organs fixed in Zenker's fluid. For comparison the macroscopical, radiological and histological examination of a normal monkey of the same species was carried out.

#### Gross Anatomical Findings.

The complete post mortem examination revealed no pathological deviations in comparison with the normal subject except for certain abnormalities of the bones of the extremities and of the parathyroid bodies. In the upper limb the humerus on both sides was bent between the upper and middle thirds to form an angle of approximately 120°. The length of each humerus measured 9 cm., the diameter at the point of bending 1.4 cm. The bone appeared to be shortened about 3 cm. but thickened about 0.5 cm. Radius and ulna on both arms measured 11 cm. in length, the same as in the normal. They were slightly bowed within the lower third. The joints of the upper limb were freely movable. In the lower limb the femur on both sides were markedly bowed and twisted in the lower third. The bones measured 9.5 cm. on the right and 10 cm. on the

left side in length and appeared to be shortened. Fibula and tibia measured 12.5 cm. in length, the same as in the normal. The fibula was of normal shape but there was bending of the shaft of the tibia. The joints of the lower limb were freely moveable except for the right knee joint which showed marked impairment of mobility due to the deformation at the lower end of the femur.

All the bones were of hard consistency. There was nowhere any thickening in the epiphyseal regions or costocartilaginous junction, nor any sign of softening. The periosteum could be easily removed from the bone and did not show any trace of inflammation or haemorrhage. Three parathyroid bodies were found. A fourth may have been encased by the thyroid, but was not detected as the thyroid was not cut into serial sections. The left upper parathyroid body was twice the length of the two others.

#### *Microscopical Findings.*

Sections were taken from the following organs: clavicle, scapula, sternoclavicular junction, humerus, femur, radius, ulna, fibula, tibia, pubic bone, calvarium, basis of skull, fifth lumbar vertebra, sternum, suprarenal, heart, thymus, thyroid, ovary, kidney, parathyroid and liver. From the histological examination of the bones, the trabeculae, particularly within the areas of bending of the femur and humerus, showed signs of active resorption and deposition of new bone substance. There was a moderate number of fractured trabeculae enveloped by numerous cells, particularly of the osteoclastic type and numerous thin-walled congested blood vessels. Other trabeculae were lined by osteoblasts on one surface and on the opposite by osteoclasts. These findings were interpreted as a structural reorganisation of the ground substance. There was, however, nowhere any sign of extensive osteoporosis or pathological bone formation, such as the mosaic structure commonly found in osteitis deformans Paget or the fibrosis of v. Recklinghausen's disease. The costocartilaginous junction and all the epiphyseal regions examined showed no pathological deviation. The bone marrow was mixed, partly cellular, partly fatty in type.

All the soft organs were normal except for the parathyroids in which the number of oxyphile cells was considerably increased (Plate I, Fig. 1).

#### *Radiological Findings.*

The X-ray examination of the bony skeleton revealed marked deformity of the long bones as a result of extensive bowing and twisting. These changes were most marked in the upper third of the humeri (Plate I,

Figs. 2, 3) and lower third of the femora. In these regions the cortex had become very thin and was associated with an increase of the medullary trabeculation. The cortex and medullary cavities of the remainder of these bones as well as the bones of the forearm and leg appeared normal.

#### *Blood Chemistry Findings.*

Calcium 10.53 mg. in serum.

Inorganic phosphorus 5.856 mg. in serum.

Bodansky phosphatase units 9.95.

Calcium/inorganic ratio 1.8.

#### DISCUSSION AND CONCLUSIONS.

Interpretation of the findings encountered some difficulties because of the lack of any pathognomonical sign. The only pathological features of the case were the deformities as revealed by gross and radiological examination, the microfractures associated with reconstruction of bone substance, previously described in the human by Looser (1920), Fromme (1921), and Salinger (1929), and finally the unusual number of oxyphile cells within the parathyroid bodies. The evaluation of the chemistry findings in the blood was difficult, because the normal figures for the green monkey are apparently not determined. In the present case they correspond approximately to that of a normal human infant and the comparatively high amount of inorganic phosphorus as well as phosphatase might be significant for a healing process of the skeleton.

Doubtless, there was no acute process acting, for the animal was in good health and softness of the bones could not be detected anywhere. It seemed rather that the monkey had previously suffered from a temporary disease associated with softening of the skeleton which had primarily affected the bones of the extremities, no doubt because the latter, as supports of the body, were particularly exposed to pressure from the body weight. After the disappearance of the noxious cause the bone substance apparently regained its normal histological features, although the deformities were never corrected. In adaption to the now altered lines of force a reorientation of the trabeculae within the deformed bones took place, with resorption of fractured or useless trabeculae and formation of new bone. In accordance with Erdheim (1914) the large number of the oxyphiles in the parathyroids were interpreted as hypertrophy necessitated by the increased demand for new bone substance.

In regard to diagnosis osteitis deformans of Paget, ostitis fibrosa v. Recklinghausen and scurvy can safely be ruled out. The condition was considered to be most probably a case of healed hungerosteomalacia—a variety of late rickets—caused by a tem-



porary deficiency in vitamin D and by insufficient exposure to sunlight. Ordinary rickets could be excluded, since the epiphyseal regions were not affected at all.

Hungerosteomalacia was observed in the adult human in Vienna, Munich and other cities of the defeated countries after the World War I by Schlesinger (1919, 1921), Wenckebach (1919), Edelmann (1919), Porges and Wagner (1919) Cramer and Schiff (1920), Heyer (1920), Steiner (1927), Eyermann (1932) and Muir Crawford (1934). The radiological appearances of the condition were described by Eisler (1919). It is associated with pain and deformities in these bones which are particularly exposed to pressure and tension such as the spine, long bones and the thoracic cage. Radiologically there is no change in mild cases, but osteoporosis, microfractures, loss of minerals have been observed in the advanced stages of the condition. Successful treatment with cod-liver oil and vitamin D was reported by Dalyell and Chick (1921) and Hume and Nirenstein (1921).

Such an interpretation of the present case seems to be justified because the monkey was doubtlessly kept on a deficient diet and had apparently been rarely exposed to sunshine. In accordance with the treatment employed in the human and that suggested by Hume, Lucas and Henderson (1929) in animals, administration of vitamin D and sufficient exposure to sunlight is recommended as preventative measure against the establishment of osteomalacia in captive animals.

#### SUMMARY.

Deformities of the long bones of all four extremities in a green monkey (*Ceropithecus sabaeus*) was found on gross and radiological examination. There was active reorganization of the trabeculae of the bones and hypertrophy of the oxyphile cells within the parathyroids. The condition was considered to be a case of healed hungerosteomalacia due to insufficient intake of vitamin D and exposure to sunshine.

The material for this study was provided by the New York Zoological Park, Bronx Park, New York City, and I want to acknowledge the kind cooperation of Dr. Leonard J. Goss in this work.

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**EXPLANATION OF THE PLATE.****PLATE I.**

- Fig. 1. Oxypyle cells of the parathyroid, including a few follicles of the thyroid.
- Fig. 2. X-ray of the right humerus showing the deformation and increased medullary trabeculation.
- Fig. 3. X-ray of the right humerus of a normal green monkey.



FIG. 1.

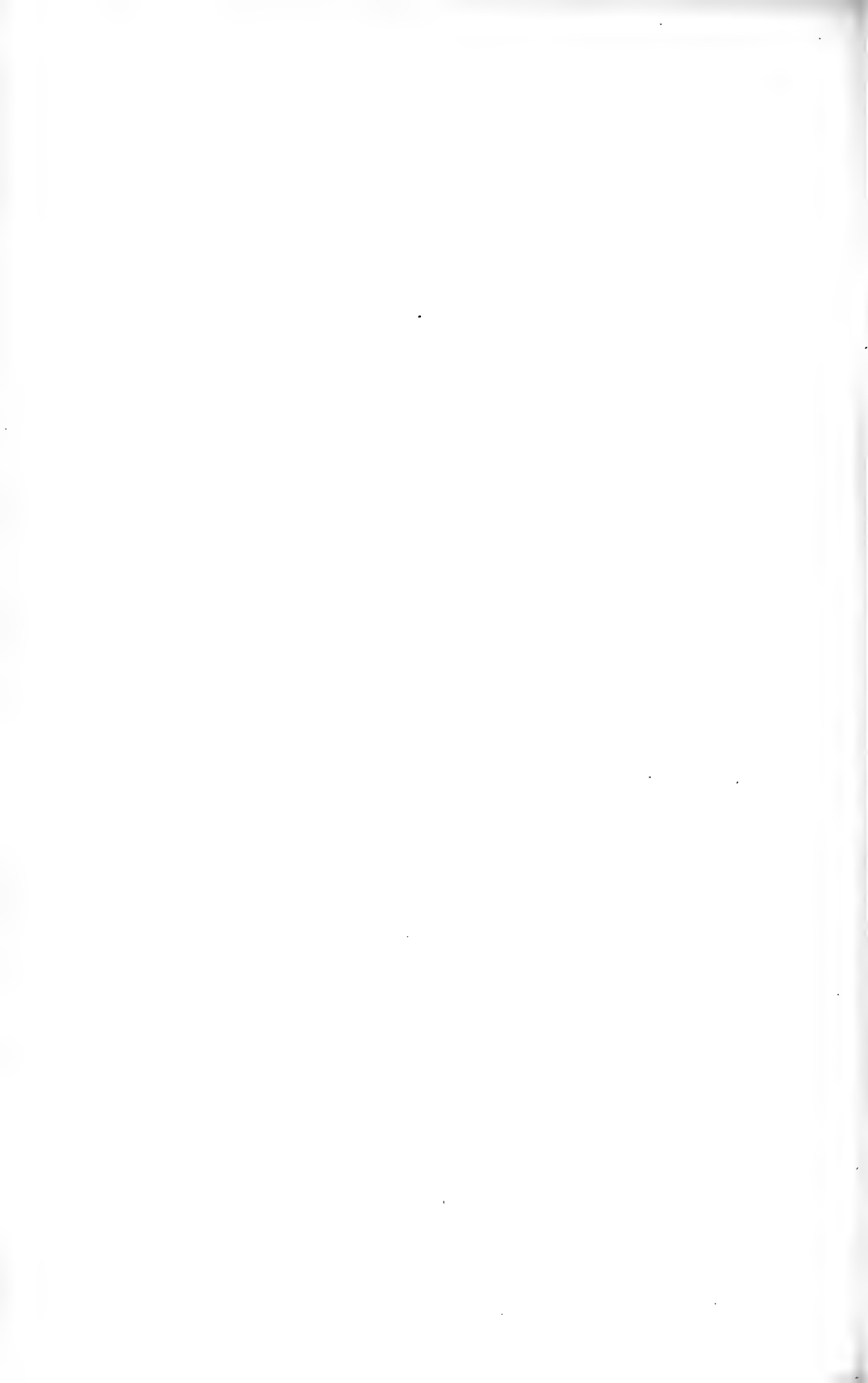


FIG. 2.



FIG. 3.

EVIDENCE OF HEALED HUNGEROSTEOMALACIA (LATE RICKETS)  
IN A GREEN MONKEY (*CERCOPITHECUS SABAEUS*).



## 19.

# Eastern Pacific Expeditions of the New York Zoological Society. XXXII. Mollusks from the West Coast of Mexico and Central America. Part. II.\*

LEO GEORGE HERTLEIN &amp; A. M. STRONG.

California Academy of Sciences.

## PLATE I.

[This is the thirty-second of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific Zaca Expedition (1937-1938). For data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14, pp. 287-298.]

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## INTRODUCTION.

In Part I of this series of papers<sup>1</sup> the authors outlined a plan for a complete catalogue of the tropical west American mollusks. Since the publication of that plan, conditions resulting from unsettled international political relations have made it necessary to change and drastically reduce the entire plan. Under the existing conditions it is thought better to record now the mollusks collected on the Zaca Expeditions, rather than to wait indefinitely for the publication of monographic reports on the fauna as a whole.

In the revised plan of publication only the species secured by the Zaca Expeditions of 1936 and 1937-1938 will receive formal headings. These will be followed by a reference to the original description and where desirable an additional reference to an illustration or to an important discussion of the species. The type locality, range, collecting stations, a brief description or de-

\*Contribution No. 671, Department of Tropical Research, New York Zoological Society.

<sup>1</sup>Hertlein, L. G., and Strong, A. M. Eastern Pacific Expeditions of the New York Zoological Society. XXII. Mollusks from the West Coast of Mexico and Central America. Part I. *Zoologica*, New York Zool. Soc., Vol. 25, Pt. 4, December 31, 1940, pp. 369-430.

scriptive notes, and the distribution will be given. Some of the species heretofore unillustrated will be figured as will the new species. Keys will include only the species collected on the *Zaca* Expeditions.

It is hoped that papers of monographic scope dealing with families of tropical west American mollusks may be published from time to time in this or in other scientific periodicals. In that way it may be possible to continue, in a modified form, the original plan of a complete catalogue of the molluscan fauna of this interesting region. The results of studies of several of the families are now in manuscript awaiting publication.

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## CLASS PELECYPODA.

### Order Prionodesmacea.

#### Superfamily Arcacea.

#### Family Glycymeridae.

#### GENUS *Glycymeris* DA COSTA

#### KEY TO THE SPECIES OF *Glycymeris*.

- A. Shell large, smooth or with fine radial striations
  - a. Color pattern of reddish-brown zigzag areas ..... *gigantea*
  - aa. Color pattern of brown dots on umbos ..... *maculata*
- B. Shell with well developed radial ribs
  - a. Ribs few, heavy, not over 12, strongly striated, with wide interspaces
    - b. Ribs rounded, not over 7 ..... *inaequalis*
    - bb. Ribs square, 9 to 11 ..... *delessertii*
  - aa. Ribs 24 to 40, not striated
    - c. Ribs 35-40 ..... *multicostata*
    - cc. Ribs fewer, not over 30
      - d. Altitude usually not over 30 mm.

- e. Hinge evenly rounded ..... *ressellata*
- ee. Hinge angulated ..... *strigilata*
- dd. Altitude over 30 mm., ribs broader ..... *canoia*

#### Subgenus *Glycymeris* s.s.

#### *Glycymeris (Glycymeris) gigantea* Reeve.

*Pectunculus giganteus* Reeve, Conch. Icon., Vol. 1, *Pectunculus*, February, 1843, species 3, pl. 1, figs. 3a, 3b. "Hab. Guaymas, Gulf of California. (Found in sandy mud at seven fathoms depth.)"

*Type Locality:* Guaymas, Mexico, in 7 fathoms, sandy mud.

*Range:* Magdalena Bay, Lower California, and from Punta Penasco, to Cape San Lucas, Lower California; Acapulco, Mexico.

*Collecting Stations:* Mexico: Santa Inez Bay, Gulf of California (145-D-1-3), 4 fathoms, sand. Also on beach and at Monument station; Cerralbo Island; Arena Point area, Gulf of California.

*Description:* Shell large, orbicular, thick, finely radially striate, ornamented by waved reddish-brown spots which touch each other and often form a zigzag pattern toward the umbos. There are about 29 or 30 hinge teeth, the central ones smaller than the distal ones. Specimens attaining a height of 100 mm. have been collected at Magdalena Bay, Lower California.

The zigzag reddish-brown color pattern serves to separate this species from *G. maculata* Broderip whose coloration consists of brown spots. The color pattern also serves to easily separate it from the Mediterranean species *G. bimaculata* Poli.

*Distribution:* The distribution of *Glycymeris gigantea* seems to be very limited. It occurs at Magdalena Bay, Lower California, and is known to occur from Pliocene to Recent in the Gulf of California region. It has been recorded from Acapulco, but it does not appear to be common south of the Gulf of California.

#### *Glycymeris (Glycymeris) maculata* Broderip.

*Pectunculus maculatus* Broderip, *Proc. Zool. Soc. London*, August 14, 1832, p. 126. "Hab. in Portu Potrero". "Found in fine gravel in eleven fathoms of water."—Reeve, Conch. Icon., Vol. 1, *Pectunculus*, 1843, species 4, pl. 1, fig. 4. "Hab. Puerto Potrero, Central America. Cuming."

*Type Locality:* Puerto Potrero, Costa Rica, in 11 fathoms, fine gravel.

*Range:* Magdalena Bay, Lower California, and Punta Penasco, Sonora, Mexico, to Zorritos, Peru.

*Collecting Stations:* Mexico: Arena Bank, Gulf of California (136-D-30), 35 fathoms, sand, weed; Cerralbo Channel (137-D-3), 46

fathoms, rock; Port Guatulco (195-D-9, 17), 6-7 fathoms, gravel, sand, crushed shell; Tangola-Tangola Bay (196-D-6, 7), 6-7 fathoms, sand, crushed shell; Nicaragua: Gulf of Fonseca, Potosi and Monypenny Point; Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: Piedra Blanca Bay (208-D-1, 10), 2-6 fathoms, rocks, sand, algae.

**Description:** The shell of *Glycymeris maculata* is large, orbicular, and ornamented by small chestnut brown spots which occur on the earlier part of the shell. This color pattern serves to separate it from *C. gigantea* Reeve. Radial striae are present on the exterior of the shell.

**Distribution:** This species occurs in shallow water from the northern part of the Gulf of California to Peru.

### Subgenus *Tuceta* Bolten.

*Tuceta* Bolten, Mus. Boltenianum, 1798, p. 172.

**Type** (here designated): "*T. pectunculus*." [In the synonymy of which Bolten included *Arca pectunculus* Gmelin, illustrated by Chemnitz, Conchyl.-Cab., Bd. 7, 1784, Tab. 58, figs. 568 and 569. Red Sea].

*Tuceta* Bolten has by some authors been placed in the synonymy of *Glycymeris* s.s. So far as we know no type has been designated heretofore for *Tuceta* and we therefore designate *Tuceta pectunculus*, in the synonymy of which Bolten placed *Arca pectunculus* Gmelin [= *Arca pectunculus* Linnaeus] illustrated by Chemnitz. This is a strongly ribbed form with an arcuate hinge. *Tuceta* thus becomes available for strongly ribbed species of *Glycymeris* similar to the type species.

### *Glycymeris (Tuceta) multicostata* Sowerby.

*Pectunculus multicostatus* Sowerby, *Proc. Zool. Soc. London*, 1832 (issued March 13, 1833), p. 195. "Hab. in America Meridionali." "Found in coarse sand and gravel, in twelve fathoms water, off the Island of Muerte, in the Bay of Guayaquil."—Reeve, *Conch. Icon.*, Vol. 1, *Pectunculus*, 1843, species 26, pl. 5, fig. 26. "Hab. Bay of Guayaquil (found in coarse sand and gravel at the depth of twelve fathoms); Cuming."

**Type Locality:** Off the Island of Muerte, Bay of Guayaquil, Ecuador, in 12 fathoms, coarse sand and gravel.

**Range:** Punta Penasco, Sonora, Mexico, to Guayaquil, Ecuador.

**Collecting Stations:** Mexico: Santa Inez Bay, Gulf of California (143-D-1; 144-D-2, also on beach), 2½-29 fathoms, mud, crushed shell, rock, weed. Cerralbo Island, Gulf of California; Arena Bank, Gulf of California (136-D-18, 27), 40-50 fathoms, mud, sand, calcareous algae, rock; Port Guatulco; Panama: Bahia Honda; Colombia: Gorgona Island.

**Description:** The shell of *Glycymeris multicostata* is elongately rounded in outline and is usually ornamented with about 35 to 40 well developed flat topped radiating ribs. The ribs vary in number and in width and in some cases are ornamented by longitudinal incised lines toward the anterior ventral margin. The ribs increase in number both by bifurcation and intercalation. On the beaks the ribbing often occurs in fascicles. The general color of the shell is gray variegated with chestnut. There is usually some brownish color in the interior of the shell, especially the posterior part.

The species described as *Pectunculus septentrionalis* by Middendorff appears to be a synonym of *Glycymeris multicostata*. Although *Glycymeris septentrionalis* has been cited in the literature as occurring in Alaska, we have seen no specimens from that region which could be referred to the species as characterized by Middendorff's original description and illustrations. Middendorff compared his species to *Glycymeris multicostata* and to the figure referred to *G. inaequalis* by Sowerby in Beechy's voyage which really represents *G. bicolor*, a form very close to *G. multicostata*. The shape, hinge, character of ribbing and color pattern in Middendorff's figures all conform with those of *G. multicostata*. The ribbing occurring in fascicles on the beaks is very characteristic of *G. multicostata*. The type specimen of Middendorff's species was said to have been collected by Wosnessensky at Ukamok Island (also known as Chirikof Island), near Kodiak, Alaska. Wosnessensky also collected in the Gulf of California, a region where *G. multicostata* occurs commonly. It appears then, unfortunately, that *Pectunculus septentrionalis* must be relegated to the synonymy of *Glycymeris multicostata*.

**Distribution:** This species occurs at many localities from the Gulf of California to Peru and is known to occur from Pliocene to Recent.

### *Glycymeris (Tuceta) tessellata* Sowerby.

*Pectunculus tessellatus* Sowerby, *Proc. Zool. Soc. London*, 1832 (issued March 13, 1833), p. 196. "Hab. ad littora Columbiae Occidentalis." "From sandy mud and gravel, in from eight to ten fathoms, at Monte Christe and in the Bay of Xipixapi."—Reeve, *Conch. Icon.*, Vol. 1, *Pectunculus*, 1843, species 29, pl. 6, fig. 29. Original locality record cited.

**Type Locality:** Monte Cristi, Ecuador, in 8 to 10 fathoms, sandy mud and gravel, here designated as type locality. Bay of Xipixapi, Ecuador, also cited originally.

**Range:** Arena Bank, northeast of Cape San Lucas, Lower California, to Xipixapi, Ecuador.

**Collecting Stations:** Mexico: Arena Bank,

Gulf of California (136-D-6, 13, 15, 18, 22, 24), 40-50 fathoms, mud, *Arca* conglomerate, sand, weed, crushed shell, muddy sand; Gorda Banks, Gulf of California (150-D-8), 40-45 fathoms, muddy sand; Manzanillo (184-D-2), 30 fathoms, gravelly sand; Port Guatulco (195-D-9), 7 fathoms, gray sand, crushed shell; Santa Cruz Bay; Costa Rica: Port Parker (203-D-1, 2, 3, also on beach), 12-15 fathoms, sandy mud, crushed shell, shelly mud; Port Culebra (206-D-1, 2, 3), 14 fathoms, sandy mud; 14 miles S. E. of Judas Point (214-D-1-4), 42-61 fathoms, mud, shell, rocks; Panama: Bahia Honda (222); Hannibal Bank.

**Description:** The shell of *Glycymeris tessellata* is triangularly orbicular, somewhat attenuated toward the umbos. The ribs, about 25 in number, are rounded and rather wide. The shell is colored by tessellated rich purple spots on a grayish-white background.

The largest specimens in this collection assigned to *Glycymeris tessellata* measure about 33.3 mm. in height. The width of the ribs appears to be somewhat variable. From the descriptions of Sowerby and Reeve there appears to be but little difference between *Glycymeris tessellata* and *strigilata* except that the latter has a more angular hinge and usually smaller ligamentary area. It is on those characters that we have separated the two forms but it is not at all certain that these are constant. Some of the forms here referred to *tessellata* have about 25 ribs, a rounded hinge with about 24 teeth which are strong on the sides but which become very weak in the center of the hinge. In a series of specimens these distinctions appear very much less pronounced and there is a suggestion of gradation from this form to those with more numerous teeth with a rounded angular hinge.

*Glycymeris pectinata* Gmelin from the Caribbean region is a similar species.

**Distribution:** This species occurs fairly commonly from the Gulf of California to Ecuador. It is also known to occur in the Pleistocene.

***Glycymeris (Tuceta) tessellata canoa*  
Pilsbry & Olsson.**

*Glycymeris canoa* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 54, pl. 13, figs. 2, 2a. "Canoa formation, Punta Blanca", Ecuador, Pliocene.

**Type Locality:** Canoa formation, Punta Blanca, Ecuador, Pliocene.

**Range:** Known living only from Arena Bank, Gulf of California.

**Collecting Station:** Mexico: Arena Bank, Gulf of California (136-D-5, 22), 33-45 fathoms, sand, weed, mud.

**Description:** This form differs from typi-

cal *tessellata* in the much greater size, extremely broad ribs and in that the color markings are more in the nature of concentric zigzag lines rather than in large spots. There are about 24 teeth on the hinge but on some large specimens there are only about 20, and the center of the hinge is nearly smooth. A typical specimen measures: height, 48.5 mm., length, 46 mm., convexity (both valves), 28.5 mm.

This subspecies appears to be a giant form of *Glycymeris tessellata* Sowerby but differs in the much greater size and broader and flatter ribs. Judging from the original description and illustrations of *Glycymeris canoa*, the specimens from the Gulf of California appear to be identical with those from the Pliocene of Ecuador.

**Distribution:** This subspecies is known living at the present time only at Arena Bank, in the southern end of the Gulf of California. It occurs in the Pliocene of Ecuador and it seems likely that it may be found living at other localities between the Gulf of California and Ecuador.

***Glycymeris (Tuceta) tessellata strigilata*  
Sowerby.**

*Pectunculus strigilatus* Sowerby, *Proc. Zool. Soc. London*, 1832 (issued March 13, 1833), p. 196. "Hab. ad Sanctam Elenam." "Dredged from a depth of six to eight fathoms in sandy mud."—Reeve, *Conch. Icon.*, Vol. 1, *Pectunculus*, 1843, species 31, plate 6, fig. 31. Original locality record cited.

**Type Locality:** Santa Elena, Ecuador, in 6 to 8 fathoms, sandy mud.

**Range:** Manzanillo, Mexico, to Santa Elena, Ecuador.

**Collecting Stations:** Mexico: Manzanillo (184-D-1-2), 25-30 fathoms, sand and gravelly sand; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, crushed shell, shelly mud.

**Description:** There appears to be little to separate the form described by Sowerby under the name "*Pectunculus strigilatus*" from that described as *P. tessellatus*. The only character cited for the form *Glycymeris t. strigilata* which may separate it from *G. tessellata* is that given by Reeve who stated "A very solid broadly ribbed shell, so peculiarly contracted towards the umbones that the hinge almost describes an angle."

In the present collection, a series of specimens dredged off Manzanillo, Mexico, seems to answer that description. The largest specimen measures 28.5 mm. from beak to base. There are about 24 to 25 ribs which in some shells are rounded but in others flattened. There are about 30 rather fine teeth which near the center of the hinge become shorter and weaker. It is uncertain whether this will prove to be a constant



character because there appears to be a gradation to forms with a rounded hinge with stronger and fewer hinge teeth. The triangular ligamentary area is generally smaller than that on typical *Glycymeris tessellata*.

The same sort of angularity of the hinge of the form *G. t. strigilata* is sometimes noticed on specimens of *G. pectinata* Gmelin.

*Distribution*: This subspecies occurs from off western Mexico to Ecuador along with *Glycymeris tessellata*.

#### Subgenus *Axinactis* Mörch.

*Axinactis* Mörch, Malakozool. Blätter, Bd. 7, 1861, p. 203. Species in original list: "*Axinaea* (*Axinactis*) *inaequalis* Sow." and "*Axinaea* (*Axinactis*) *assimilis* Sow.?"

*Type* (here designated): *Axinaea* (*Axinactis*) *inaequalis* Sowerby.

Shell roundly triangular, thick, beaks opisthogyrate; ribs wide and separated by narrower interspaces; ribs, interspaces and margins covered by fine radial ribs which are separated by fine incised lines; cardinal area forming an elongate asymmetric triangle and ornamented by six or seven incised lines which run diagonally to the base from an impressed line bordering the posterior part of the area; only a small portion of the ligament occurs in front of the beaks; hinge with two series of chevron-shaped teeth, the two series separated by an impressed line which is almost directly in line with the beaks; the posterior portion of the anterior series small and nearly vertical; on perfectly preserved specimens a fine row of denticles is present along the rather straight portion of the posterior margin; inner margin of valves fluted.

#### *Glycymeris* (*Axinactis*) *delessertii* Reeve.

*Pectunculus delessertii* Reeve, Conch. Icon., Vol 1, *Pectunculus*, December, 1843, species 52, pl. 9, fig. 52. "Hab.—?"

*Glycymeris delesserti* Reeve, Pilsbry & Lowe, *Nautilus*, Vol. 47, No. 3, 1934, p. 85. Maria Madre Island, Tres Marias Islands, Mexico.

*Type Locality*: No locality originally cited. Maria Madre Island, Tres Marias Islands, Mexico, here designated as type locality.

*Range*: Mazatlan, Mexico, to Panama.

*Collecting Station*: Mexico: Port Guatulco, on beach.

*Description*: A worn left valve of *Glycymeris delessertii* is present in the collection from Port Guatulco, Mexico. The shell of this species is ornamented by about 9 to 11 squarish ribs which are separated by interspaces a little narrower. The ribs are ornamented by riblets separated by longitudinally incised lines varying in depth and number. These incised lines continue over

the interspaces on the anterior and posterior portions of the shell but in the median portion the interspaces are only finely striated.

The more numerous, narrower, square ribs easily separate this species from *Glycymeris inaequalis* Sowerby.

*Distribution*: This species has been collected at Mazatlan, the Tres Marias Islands, Port Guatulco, Mexico, and at Panama. It is also known to occur in the Pleistocene of Oaxaca, Mexico.

#### *Glycymeris* (*Axinactis*) *inaequalis* Sowerby.

*Pectunculus inaequalis* Sowerby, *Proc. Zool. Soc. London*, 1832 (issued March 13, 1833), p. 196. "Hab. ad Panamam et Real Llejos." "Found in sandy mud in ten fathoms."—Reeve, Conch. Icon., Vol. 1, *Pectunculus*, 1843, species 16, pl. 4, fig. 16. Original locality record cited.

*Type Locality*: Panama City, Panama, in 10 fathoms, sandy mud, here designated as type locality. Real Llejos [near Corinto], Nicaragua, also cited originally.

*Range*: San Marcos Island, Gulf of California, to Bayover, Peru.

*Collecting Stations*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: Piedra Blanca Bay (208-D-1, 10), 2-6 fathoms, rocks, sand, algae.

*Description*: This species is readily recognized by the presence of about 6 rather broad, rounded ribs which on the anterior and posterior portions of the shell give way to one or two small ribs. The ribs are wider than the interspaces and both are covered by small somewhat irregular riblets which are due to the presence of incised lines. The color of the exterior of the shell is a whitish background with irregular concentric bands of dark brown color.

*Glycymeris inaequalis* can be separated from *G. delessertii* by the presence of the fewer, broader, rounded ribs. The species described as *Pectunculus assimilis* by Sowerby can be relegated to the synonymy of *Glycymeris inaequalis*.

*Distribution*: This species has been recorded from various localities from the Gulf of California to Peru. It is also known to occur in the Quaternary of Ecuador.

#### Family Arcidae.\*

#### KEY TO THE GENERA AND SUBGENERA OF THE ARCAIDAE.

- A. Beaks curved toward the anterior....*Arca*  
a. Inner margin of valves smooth

\*For a classification of the Arcidae, see Reinhart, P. W., "Classification of the Pelecypod Family Arcidae," *Bull. Mus. Roy. Hist. Nat. Belgique*, Tome 11, No. 13, 1935, 68 pp., pls. 1-5.

Another important paper published recently by Reinhart is entitled "Mesozoic and Cenozoic Arcidae from the Pacific Slope of North America," *Geol. Soc. America, Special Papers* No. 47, June 16, 1943, pp. XI, 1-117, pls. 1-15, 3 figs. in text, 3 tables.

- b. Hinge with a continuous series of teeth
- c. Ligamental area extremely wide and almost flat; posterior end more or less expanded. *Arca* s.s.
- cc. Ligamental area narrow, V-shaped
- d. Ligamental area extending equally on each side of the umbos ..... *Barbatia*
- dd. Ligamental area extending mainly posterior to the umbos
- e. Muscle scars prominent, elevated; anterior and posterior ribs not larger than the others ..... *Acar*
- ee. Muscle scars not prominent; large anterior and posterior ribs ..... *Calloarca*
- bb. Hinge with an edentulous pit or gape in the middle ..... *Arcopsis*
- aa. Inner margin of valves crenulated
- f. Right and left valves equal in size and sculpture
- g. Ligamental area extending equally on each side of the umbos
- h. Central teeth perpendicular to the hinge line. *Anadara*
- hh. Central teeth diverging ..... *Larkinia*
- gg. Ligamental area extending mainly posterior to the beaks ..... *Lunarca*
- ff. Left valve the larger, overlapping the right
- i. Posterior dorsal margin with a flattened auriculation ..... *Cara*
- ii. Posterior dorsal margin without a flattened auriculation
- j. Sculpture of the two valves similar or only slightly different ..... *Scapharca*
- jj. Sculpture of the two valves strongly discrepant ..... *Cunearca*
- B. Beaks curved toward the posterior. *Noetia*
- a. Shell trigonal ..... *Noetia* s.s.
- aa. Shell elongate
- b. Posterior end strongly expanded ..... *Sheldonella*
- bb. Posterior end not expanded. *Eontia*

# GENUS *Arca* LINNAEUS.

## Subgenus *Arca* s.s.

### KEY TO THE SPECIES OF *Arca* s.s.

- A. Shell expanded posteriorly; posterior margin notched ..... *pacifica*

- B. Shell not expanded or notched posteriorly but obliquely truncated or rounded ..... *mutabilis*

## *Arca (Arca) fernandezensis* Hertlein & Strong, nom. nov.

*Arca angulata* King & Broderip, *Zool. Jour.*, Vol. 5, July, 1832, p. 336. "Habitat ad Juan Fernandez." "This shell was dredged up from 80 fathoms water in the offing of Cumberland Bay, at Juan Fernandez; it was attached to a branch of coral."—Stempell, *Zool. Jahrb.*, Suppl. Bd. 5, December 20, 1899, Fauna Chilensis, Bd. 2, p. 219, pl. 12, figs. 1-9. Juan Fernandez Island, on rocks along the coast and in 20 to 40 fathoms.

Not *Arca angulata* Meuschen, Mus. Gev., 1787, p. 426.

A study of the west American species of Arcidae revealed that the specific name *angulata* of King and Broderip had been used earlier for a species of *Arca* by Meuschen. The new name *Arca fernandezensis* is here proposed for the species from Juan Fernandez Island.

## *Arca (Arca) mutabilis* Sowerby.

*Byssarca mutabilis* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 17. "Hab. in Colombia occidentali." "Found under stones at the Isle of Plata".

*Arca mutabilis* Sowerby, Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 85, pl. 13, fig. 85. Original locality record cited.

*Type Locality*: Island of La Plata, Ecuador, under stones.

*Range*: Magdalena Bay, Lower California, and the Gulf of California, to Guayaquil, Ecuador.

*Collecting Stations*: Mexico: Arena Bank, Gulf of California (136-D-21), 45 fathoms, mud; Port Guatulco; Sihuatanejo; Costa Rica: Port Parker; Port Culebra; Piedra Blanca; Isla Cedro.

*Description*: The four to six ribs on the posterior slope of the shell of *Arca mutabilis* are somewhat coarser than the others and in fresh shells these are characteristically dark in color. The ligamentary area is concave.

*Arca mutabilis* is strikingly like *A. imbricata* Bruguière of the western Pacific. Lamy considered the two forms to differ only subspecifically. *Arca santamariensis* Reinhart from the Pliocene of California is similar to *A. mutabilis* but is said to differ in ornamentation and in the shape of the ligamental area.

*Distribution*: This species is often found under rocks at low tide from Magdalena Bay, Lower California, and the Gulf of California, to Ecuador.

***Arca (Arca) pacifica* Sowerby.**

*Byssarca pacifica* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 17. "Hab. ad Sanctam Elenam." "Found on rocky ground, in from six to eighteen fathoms, adhering to each other in large bunches."

*Arca pacifica* Sowerby, Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 75, pl. 11, fig. 75. Original locality record cited.

**Type Locality:** Santa Elena, Ecuador, in 6-18 fathoms, on rocky ground.

**Range:** Scammon Lagoon, Lower California, to Paita, Peru, and the Galápagos Islands.

**Collecting Stations:** Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand; Santa Inez Point, Lower California; Arena Bank, Gulf of California (136-D-1, 17), 45 fathoms, mud and *Arca* conglomerate; Arena Point area, Lower California; Gorda Banks, Gulf of California (150-D-7-8, 16), 20-75 fathoms, sand, muddy sand, rock, calcareous algae; Cape San Lucas, Lower California; Passavera Island, Chamela Bay; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves on bottom; Costa Rica: Port Parker; Piedra Blanca (208-D-1-10), 2-6 fathoms, rocks algae, sand; Panama: Hannibal Bank; Bahía Honda; Colombia: Gorgona Island.

**Description:** The shell of *Arca pacifica* is expanded and notched posteriorly. It is ornamented by radiating ribs and is colored by narrow, rounded V-shaped brown bands. It is more expanded posteriorly than *A. occidentalis* Philippi, a species living in the Caribbean region.

**Distribution:** This species often occurs from Scammon Lagoon, Lower California, to Peru, under rocks at very low tide and in shallow water. It also occurs in the Pliocene and Pleistocene of Lower California.

**Subgenus *Acar* Gray.*****Arca (Acar) gradata* Broderip & Sowerby.**

*Arca gradata* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, January, 1829, p. 365. "Hab. ad littora Oceani Pacifici." Also "From Mazatlan."

*Barbatia (Acar) gradata* Sowerby, Reinhardt, *Trans. San Diego Soc. Nat. Hist.*, Vol. 9, No. 10, 1939, pp. 39-43, pl. 3, figs. 1a, 1b, 5a, 5b, 6a, 6b, 6c, 6d, 6e. Mazatlan, Mexico, and Taboga Island, Panama.

**Type Locality:** Pacific Ocean, littoral. Also Mazatlan. [Mazatlan, Mexico, stated to be the type locality by Reinhart and accepted as such by the present authors].

**Range:** Point Abreojos, Lower California, to Punta Penasco, Sonora, Mexico, and south to Negritos, Peru, and the Galápagos Islands.

**Collecting Stations:** Mexico: Cape San Lucas, Lower California; Sulphur Bay,

Clarion Island; Banderas Bay; Port Guatuleco (195-D-9, 15), 1.5 to 7 fathoms, gray sand, crushed shell, coral; Tangola-Tangola Bay (196-D-14-15, and beach), 5 fathoms, crushed shell; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves on bottom; Costa Rica: Port Parker; Ballena Bay; Uvita Bay.

**Description:** Shell moderately thick for its size, ornamented exteriorly by reticulate sculpture. On some specimens granules are developed at the point where the concentric crosses the radial sculpture. At the time of of the original description of the species Broderip & Sowerby stated, "This elaborately ornamented shell looks at first sight like a piece of Chinese carving." Large specimens attain a length of about 30 mm.

The first published figure of *Arca gradata* is in the Zoology of Beechy's Voyage, 1839, p. 152, pl. 43, fig. 1. The part of that work here involved was prepared by Sowerby so the specimen may be considered to be authentic in the absence of information to the contrary. This figure shows a coarsely sculptured shell. This interpretation of the species is identical with that of Reinhart who has discussed and illustrated the holotype.

*Arca gradata* closely resembles *A. reticulata* Gmelin, a Caribbean species, and there are somewhat similar species in the Western Pacific.

**Distribution:** This species occurs from Lower California to Peru and the Galápagos Islands. It is often found under rocks between tides.

**Subgenus *Anadara* Gray.****KEY TO THE SPECIES OF *Anadara*.**

- A. Anterior dorsal margin acutely pointed; about 30 ribs.....*biangulata*
- B. Anterior dorsal margin forming nearly a right angle, or rounded
  - a. Anterior ribs deeply grooved, finely nodulous.....*formosa*
  - aa. Anterior ribs not grooved or only faintly so
  - b. Ribs 35-37
    - c. Ribs tuberculated, shell high tuberculosa
    - cc. Ribs smooth, shell elongate mazatlanica
  - bb. Ribs 40-44.....*similis*

***Arca (Anadara) biangulata* Sowerby.****Plate I, Figure 3.**

*Arca biangulata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 21. "Hab. ad littora Columbiae Occidentalis. (Atacamas)," "A single specimen was dredged at a depth of seven fathoms."

*Arca gordita* Lowe, *Trans. San Diego*

*Soc. Nat. Hist.*, Vol. 8, No. 6, March 21, 1935, p. 16, pl. 1, fig. 1. "Acapulco, 20 fathoms" (type). Also "Guaymas, 20 fathoms" and "off West Mexico."—R. H. Palmer & Hertlein, *Bull. South. Calif. Acad. Sci.*, Vol. 35, pt. 2, May-August [issued September 10], 1936, p. 70, pl. 19, figs. 1 and 4. Pleistocene of Oaxaca, Mexico.

*Type Locality*: Atacames, Western Ecuador, dredged in 7 fathoms. Of *Arca gordita*, Acapulco, Mexico, in 20 fathoms.

*Range*: Guaymas, Sonora, Mexico, to Paita, Peru, and the Galápagos Islands.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (143-D-1, 5), 18-29 fathoms, sand, mud, crushed shells, weeds; Gorda Banks, Gulf of California (150-D-8), 40-45 fathoms, muddy sand; Manzanillo Bay (184-D-2), 30 fathoms, gravelly sand; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, shelly mud, and crushed shells; 14 miles southeast of Judas Point (214-D-1 to 4), 42-61 fathoms, mud, shell, rocks; Panama: Gulf of Chiriqui (221-D-1 to 5), 35-40 fathoms, sandy mud.

*Description*: *Arca biangulata* was originally described by Sowerby as oblong, ventricose, white, radiately ribbed, covered by a brown periostracum, dorsal margin anteriorly acute, posteriorly obtusely angulated; anterior end shorter and higher; posteriorly subacuminate; ligamentary area elongate, flat, wider anteriorly. Length, 2.0; width, 1.2; height, 1.3 poll.

That description exactly applies to the shell described by Lowe as *Arca gordita*. The shell is sharply pointed anteriorly and is ornamented by about 30 ribs. Palmer and Hertlein have pointed out the resemblance of this form to Miocene species of the Caribbean region.

*Distribution*: This species is now known to occur from the Gulf of California to Peru. It is also known to occur in the Pleistocene of Oaxaca, Mexico.

#### *Arca (Anadara) formosa* Sowerby.

*Arca formosa* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 20. "Hab. in America Centrali. (Gulf of Tehuantepec)." —Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1843, species 10, pl. 2, fig. 10. "Hab. Gulf of Tehuantepec, Mexico (found in sandy mud at the depth of from ten to twelve fathoms); Cuming."

*Type Locality*: Gulf of Tehuantepec, Mexico.

*Range*: Cedros Island, off Lower California, to Paita, Peru.

*Collecting Stations*: Mexico: East of Cedros Island (126-D-6), 45 fathoms, mud; Tangola-Tangola Bay (196-D-6-7), 6-7 fathoms, sand and crushed shell; El Salvador: La Union; Costa Rica: Culebra Bay; Piedra Blanca.

*Description*: Shell elongate, posterior dorsal area rather broad and somewhat concave, ornamented by about 35 to 38 flat-topped ribs. The posterior ribs are wider, the anterior ones finely nodulous and divided by a groove.

Two specimens referable perhaps to this species were dredged about 3 miles east of Cedros Island. A specimen from La Union, Gulf of Fonseca, El Salvador, measures 112.3 mm. in length.

*Distribution*: This species is known to occur from Cedros Island, Lower California, to Peru, but is not very abundant in any of the collections which we have studied.

#### *Arca (Anadara) mazatlanica* Hertlein & Strong, sp. nov.

Plate I, Figures 1 and 4.

Shell elongately-oval, moderately convex, equivalve, white under a brown epidermis which is thin and rubbed near the beaks, thicker toward the margin and fringed in the interspaces between the ribs; hinge line straight with beaks rising above it at about the anterior third; anterior end forming almost a right angle at the end of the hinge line, then slightly rounded; posterior end forming an obtuse angle at the end of the hinge line, roundly pointed at the junction with the basal margin which is slightly convex and without a gape; sculpture of 35 broad, smooth, flat-topped ribs with narrow interspaces; ligamental area fairly broad, with 4 incised lines angulated under the beaks in such a manner as to leave a smooth, flattened shelf along the anterior dorsal margin; hinge with about 60 narrow teeth extending about the full length of the hinge line, small, vertical and closely spaced in the middle, larger, wider spaced and slightly oblique towards the ends. The type measures: longitudinal diameter, 62 mm., vertical diameter, 36.3 mm.; convexity of the two valves, 31 mm.

Holotype, and paratypes (Calif. Acad. Sci. Paleo. Type Coll.), dredged at Station No. 153-D-2, in approximately Lat. 23°06'N., Long. 106°47'W., 19 miles west of Mazatlan, Mexico. Twenty additional specimens were dredged in the same locality. In the same general locality six specimens were dredged at Station 153-D-3. Three odd valves were dredged at Station 155-D-1, in 56 fathoms thirteen miles west of Mazatlan, Gulf of California, Lat. 23°12'N., Long. 106°40'W., in 56 fathoms in mud. One specimen was dredged at 143-D-5, Lat. 26°54'N., Long. 111°53'W., Santa Inez Bay, Lower California, in 18 fathoms in sand.

*Range*: Santa Inez Bay, east coast of Lower California, to off Mazatlan, Mexico.

In many ways this species resembles *Arca formosa* Sowerby but the anterior end is shorter and more sharply angulated at the

hinge line. Also the ribs show no indication of a median groove. The ventral margin of the new species is rounded while that of *Arca formosa* is nearly straight. The new species bears a resemblance to *Arca concinna* but it is a higher shell, the anterior end is more obliquely rounded and the basal margin is more swollen and rounded.

The new species also bears a close resemblance to "*Barbatia (Diluvarca) halidonata oresta*" Woodring<sup>2</sup> but seems to have wider ribs than the east coast fossil. *Arca springvalensis* Vokes<sup>3</sup> from the Miocene of Trinidad is also somewhat similar in its general features.

*Arca scticostata* Reeve is somewhat similar to *A. mazatlanica*. Tomlin cited "*Anadara scticostata*" Reeve<sup>4</sup> from Coiba Island, Panama. That record can probably be referred to *Arca formosa* or to some similar but different West American species.

#### *Arca (Anadara) reinharti* Lowe.

*Arca (Anadara) reinharti* Lowe, *Trans. San Diego Soc. Nat. Hist.*, Vol. 8, No. 6, March 21, 1935, p. 16, pl. 1, figs. 3a, 3b, 3c. "Guaymas, 20 fathoms" (type). P. 27, Punta Penasco, Sonora, Mexico, dredged in 10 fathoms.

*Type Locality*: Guaymas, Mexico, in 20 fathoms.

*Range*: Punta Penasco, Sonora, Mexico, to Bahia Honda, Panama.

*Collecting Stations*: Mexico: Manzanillo (184-D-2), 30 fathoms, gravelly sand; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves on bottom; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, shelly mud, algae; Panama: Gulf of Chiriqui (221-D-1), 35 fathoms, sandy mud; Bahia Honda.

*Description*: The specimens here referred to *Arca reinharti* appear to be identical with a paratype No. 4697a of that species in the collection of the California Academy of Sciences. The present specimens appear to be a little longer than the type of *A. reinharti* as figured by Lowe. The type was described as possessing about 25 ribs. The specimens in the present collection have about 27 ribs which would appear to fall within the variation of the species. Some specimens are much thinner than others and the ribs are smoother but otherwise they appear to be identical with typical *A. reinharti*.

*Arca reinharti* bears a considerable resemblance to young specimens of *A. multi-*

*costata* Sowerby. Both are slightly inequivalve, the left valve over-lapping the right. The shells of *A. reinharti* are more elongate and have about 10 less ribs.

*Distribution*: This species is known to occur from the Gulf of California to Panama. In some localities it is fairly abundant in 10 to 35 fathoms, especially off Manzanillo, Mexico, and off Port Parker, Costa Rica.

#### *Arca (Anadara) similis* C. B. Adams.

Plate I, Figures 2 and 5.

*Arca similis* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, 1852, p. 485 (separate p. 261). "Panama."

*Type Locality*: Panama.

*Range*: Corinto, Nicaragua, to Panama.

*Collecting Stations*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves on bottom; Costa Rica: Port Culebra; Puntarenas Lagoon.

*Description*: The shell of *Arca similis* was described by Adams as having 40 to 44 ribs. The specimens which we identify as this species have about 40 ribs. They differ from *Arca tuberculosa* Sowerby in that Adams's species is not as high in proportion to the length, the umbonal ridges are rounded and the dorsal margin is rounded at each end.

The species *Arca tuberculosa* and *A. similis* occur together and they are quite similar in general features but they appear to be separable at least in adult forms. Carpenter considered *A. similis* to be "scarcely a variety of *A. tuberculosa*."

*Distribution*: The present record of this species from Corinto, Nicaragua, is an extension northward of the range. It is also known to occur off Costa Rica and Panama.

#### *Arca (Anadara) tuberculosa* Sowerby.

*Arca tuberculosa* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 19. "Hab. ad Real Llejos." "Found at low water at the roots of the mangrove trees." — Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 18, pl. 3, fig. 18. Original locality record cited.

*Type Locality*: Real Llejos [near Corinto], Nicaragua, at low water at the roots of mangrove trees.

*Range*: Ballenas Lagoon, Lower California, and the Gulf of California, to Tumbes, Peru.

*Collecting Stations*: Costa Rica: Port Culebra; Culebra Bay; Ballena Bay; Golfito Bay; 1 mile south of Golfito Bay; Panama: Isla Partida; Colombia: Gorgona Island.

*Description*: Shell large, elongately ovate, moderately inflated, moderately thick, and ornamented by about 33 to 37 ribs which are tuberculate toward the margin and especially so anteriorly. The dorsal margin of the shell is usually somewhat angulated at either end.

<sup>2</sup> *Barbatia (Diluvarca) halidonata oresta* Woodring, *Carnegie Inst. Washington. Publ.* 366, May, 1925, p. 43, pl. 4, figs. 5 and 6. Bowden, Jamaica, Miocene.

<sup>3</sup> *Anadara (Anadara) springvalensis* Vokes, *Amer. Mus. Novitat.*, No. 988, May 16, 1938, p. 10, fig. 3. Springvale, Trinidad. Upper Miocene.

<sup>4</sup> *Anadara scticostata* Reeve, Tomlin, *Jour. Conch.*, Vol. 18, No. 7, May, 1928, p. 189. "Coiba, valves dredged in 10-12f." See *Arca scticostata* Reeve, *Conch. Icon.*, Vol. 2, *Arca*, February, 1844, sp. 38, pl. 6, fig. 38. "Hab. —?"

Compared to *Arca similis* C. B. Adams, *A. tuberculosa* is higher in proportion to the length, more angulated at the ends of the dorsal margin, and the posterior umbonal area is more angular.

This species is commonly used for food along the west coast of Central America. At La Union, El Salvador, these shells are known as "coriles" and in Nicaragua as "tuchia." It is the "concha prieta" of Peruvian fishermen.

**Distribution:** This species occurs commonly from the Gulf of California to Peru. It often occurs abundantly in soft mud of mangrove swamps. It has been cited as occurring in archaeological ruins and kitchen middens of southwestern United States.

### Subgenus *Arcopsis* von Koenen.

#### *Arca (Arcopsis) solida* Sowerby.

*Byssosarca solida* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 18. "Hab. ad Paytam, Peruviae." "Found under stones."

*Arca solida* Sowerby, Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 106, pl. 16, fig. 106. Original locality record cited.

**Type Locality:** Paíta, Peru, under stones.

**Range:** Asuncion Island. Lower California, Mexico, and the Gulf of California, to Paíta, Peru, and the Galápagos Islands.

**Collecting Stations:** Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves on bottom; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud.

**Description:** Shell small, somewhat inflated, subquadrate, with many fine radial ribs. It may be distinguished from other similar shells by the character of the ligament which is restricted to a small triangular pit beneath the beaks and by the lack of teeth in the central part of the hinge.

*Arca solida* is very similar to *A. afra* Gmelin, an African species. Lamy considered the two forms to be only subspecifically different.

Maury has mentioned a similarity between *A. solida* and *A. adamsi* (Shuttleworth) Smith from the upper Miocene and Pliocene of Trinidad, and Recent from North Carolina to Brazil.

**Distribution:** *Arca solida* occurs commonly from the Gulf of California to Peru, under rocks between tides.

### Subgenus *Lunarca* Gray.

#### *Arca (Lunarca) vespertina* Mörch.

Plate I, Figures 6 and 7.

*Arca (Argina) vespertina* Mörch, *Malakozool. Blätter*, Bd. 7, 1861, p. 204. "Realejo in Cribra oblecta valv. sinistra fracta, an juvenilis?" — Kobelt, *Martini-Chemnitz Conchyl.-Cab.*, Bd. 8, Abt. 2, *Arca*, 1891, p. 225. Original record cited.

**Type Locality:** Realejo [near Corinto], Nicaragua.

**Range:** Mazatlan, Sinaloa, Mexico, to Corinto, Nicaragua.

**Collecting Station:** Nicaragua: Corinto (200-D-17, 19), 7-13 fathoms, sand, mangrove leaves.

**Description:** "T. alba quadrangularis postice lata, fere perpendiculariter recte truncata, angulo inferiore rotundato; margo dorsalis rectus, ventralis antice leviter adscendens; costis circiter 38 approximatis, unde margine interno profunde sulcato; umbonis coerulescentibus, radiis obscuris tribus quorum posticis subconfluentibus. Long. 7 3/4, alt. 6 1/4 mill." (Original description).

Mörch compared *Arca vespertina* to *Arca obliqua* Reeve, a species from West Africa which it somewhat resembles in shape.

The shell described by Mörch was apparently a juvenile specimen. Specimens studied by us from Corinto, Nicaragua, and from off Mazatlan, Mexico, seem to be referable to *Arca vespertina*. Small specimens agree closely with Mörch's description. Large specimens are much more elongate in proportion to the height of the shell. There are from 36 to 38 ribs which are medially sulcated toward the ventral margin. The color of the shell is white with a black spot on the beak and the shell is covered by a dark brown periostracum.

*Arca brevifrons bucaruana* Maury & Sheldon is very similar but is more quadrate in shape, thicker, and with about 33-35 ribs.

The three forms, *Arca brevifrons*, *A. brevifrons bucaruana* and *A. vespertina*, appear to be closely related, differing in the number of ribs. The Peruvian form *brevifrons* possesses 22-23 ribs, *bucaruana* from Panama with 33-35 ribs, and *vespertina* from Central America and Mexico with 36-38 ribs. The species described as *Arca (Barbatia?) melanoderma* by Pilsbry & Lowe appears to be referable to *Arca brevifrons bucaruana*.

**Distribution:** This rare species has been found only occasionally from Mazatlan, Mexico, to Corinto, Nicaragua.

### Subgenus *Barbatia* Gray.

#### *Arca (Barbatia) reeveana* d'Orbigny.

*Arca helbingii* Bruguière, Reeve, *Conch. Icon.*, Vol. 2, *Arca*, April, 1844, species 90, pl. 14, fig. 90. "Hab. St. Elena and Monte Christi, West Columbia, and island of Corrigidor, Philippines (found under stones at low water); Cuming."

*Arca reeveana* d'Orbigny, *Voy. Amér. Mérid.*, Vol. 5, 1846, p. 635. "a été rencontrée à Payta (Pérou) par M. Fontaine, et à Monte-Cristi (république de l'Equateur), par M. Cuming." [Not the record Corrigidor, Philippine Islands]. New name for *Arca*



*helbingii* Bruguière, Reeve, 1844, pl. 14, fig. 90, not *Arca helbingii* Bruguière, 1792.

*Type Locality:* Santa Elena, Ecuador, here designated as type locality. Monte Cristi, Ecuador, also cited originally.

*Range:* Manuela Lagoon, Lower California, and Punta Penasco, Sonora, Mexico, to Zorritos, Peru.

*Collection Stations:* Mexico: Santa Inez Bay, Gulf of California; Arena Bank, Gulf of California (136-D-4), 55 fathoms, mud; Costa Rica: Ballena Bay.

*Description:* Shell large, variable in shape, attaining a length of 65 mm., oblong, often very sinuate at the ventral margin, moderately thin for the group, beaks often nearly central; sculpture of radiating threads crossed by concentric lines which, where they cross the radials, cause beading, especially on the center of the valves, ribs usually coarser along the posterior dorsal margin; hinge arcuate, with the central teeth fine and closely-set, the distal teeth are larger, longer, and oblique; ligament occupying the entire cardinal area; diamond-shaped grooves on the area are closely set.

The sculpture of *Arca reeveana* is in its general features similar to that of *Arca candida* Gmelin of the Caribbean region, and *Arca velata* Sowerby and *A. decussata* from the Indo-Pacific region. *Arca platensis* Philippi from the Tertiary of Patagonia is a related species as is *A. subhelbingi* d'Orbigny from the Miocene of France.

*Distribution:* This species occurs commonly from the Gulf of California to Peru, and is found attached to the under surfaces of rocks at low tide.

### Subgenus *Calloarca* Gray.

#### *Arca (Calloarca) alternata* Sowerby.

*Byssoarca alternata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 17. "Hab. in Columbia occidentali." "Found attached to stones, on a rocky bottom, in twelve fathoms."

*Arca alternata* Sowerby, Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 88, pl. 13, fig. 88. Original locality record cited.

*Type Locality:* Western Colombia, in 12 fathoms, on rocky bottom.

*Range:* Punta Penasco, Sonora, Mexico, to Ecuador.

*Collecting Stations:* Mexico: Santa Inez Bay, Gulf of California (145-D-1, -3, and shore), 4-13 fathoms, sand; Nicaragua: Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, crushed shell, shelly mud.

*Description:* Shell thin, elongate, somewhat contracted medially and with a sharply carinated posterior umbonal slope. It is ornamented by 26 to 28 ribs and those posterior to the carinated portion, the three on the anterior end of the shell are coarse

and crenulated. On the medial portion of the shell the ribs are flat, smooth, close-set and divided down the middle by a fine incised line. The cardinal area is long and narrow, and wider in front of the beaks. The ligament occupies only the posterior part of the area.

*Distribution:* This is not a common species but is known to occur from the Gulf of California to Ecuador. It is also known to occur in the Pleistocene of Magdalena Bay, Lower California.

### Subgenus *Cara* Gray.

#### *Arca (Cara) emarginata* Sowerby.

*Arca emarginata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 20. "Hab. ad littora Maris Pacifici." "From Atacamas, Real Llejos, Xipixapi, Panama, and the Gulf of California."—Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 26, pl. 4, fig. 26. Original locality records cited.

*Type Locality:* Atacamas, Ecuador, here designated as type locality. Pacific Ocean littoral, Xipixapi, Ecuador, Panama, and the Gulf of California, also cited originally.

*Range:* Gulf of California, to Guayaquil, Ecuador.

*Collecting Station:* Nicaragua: Corinto (200-D-11, 19), 8-13 fathoms, mangrove leaves on bottom.

*Description:* Shell thin, elongate, anterior end very short, posterior end produced and with a distinct notch just below the hinge line in the upper posterior margin; the color is white with usually a black ray on the sulcated beaks; ribs 28 to 30, flat and closely-set, divided by very narrow interspaces; anterior ribs more or less medially grooved and crenulate, the ribs over the umbonal ridge are wider; cardinal area long, narrow, and somewhat wider anteriorly; teeth very fine on the center of the hinge but longer and larger distally, especially toward the posterior end. The shell attains a length of at least 50 mm.

This species is somewhat similar to *Arca esperanza* Maury from the Miocene of Trinidad.

*Distribution:* This species is found occasionally from the Gulf of California to Ecuador. It is also known to occur in the Pleistocene of Magdalena Bay, Lower California.

### Subgenus *Cunearca* Gray.

#### KEY TO THE SPECIES OF *Cunearca*.

- A. Shell with 30 or more ribs
  - a. Shell thin, posteriorly produced *aequatorialis*
  - aa. Shell thick, only slightly posteriorly produced *bifrons*
- B. Shell with less than 30 ribs

- a. Cardinal area with chevron-shaped grooves; 26-28 ribs.....*esmeralda*
- aa. Cardinal area without chevron-shaped grooves
  - b. Beaks and apex of area central, 28 ribs.....*perlabiata*
  - bb. Beaks and apex of area anterior, about 22-23 ribs.....*nux*

***Arca (Cunearca) aequatorialis* d'Orbigny.**

*Arca ovata* Reeve, Conch. Icon., Vol. 2, *Arca*, February, 1844, species 49, pl. 8, fig. 49. "Hab. St. Elena, South America (found in sandy mud at the depth of from six to eight fathoms); Cuming."

*Arca aequatorialis* d'Orbigny, Voy. Amér. Mérid., Vol. 5, 1846, p. 636. Santa Elena, Ecuador. New name for *Arca ovata* Reeve, not *Arca ovata* Gmelin, 1791.

**Type Locality:** Santa Elena, Ecuador, in 6 to 8 fathoms, sandy mud.

**Range:** Mazatlan, Mexico, to Zorritos, Peru, and the Galápagos Islands.

**Collecting Stations:** Guatemala: 7 miles west of Champerico (197-D-1-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1-2), 13-14 fathoms, mud; Nicaragua: Corinto (200-D-10, 19), 7-13 fathoms, mangrove leaves on bottom; Panama: Gulf of Chiriqui (221-D-1,-5), 35-40 fathoms, sandy mud.

**Description:** The shell of this interesting species is moderately thin and inequivalved. The color is white but often stained with reddish-brown. The ribs are about 30 to 32 in number, those on the left valve are broader than those on the right. The ribs on the anterior area are coarsely nodose, those on the posterior area are flat, smooth, and less prominent.

*Arca aequatorialis* differs from *A. bifrons* Carpenter, in the smaller, thinner shell which is more produced posteriorly and ornamented with more coarsely nodose ribs anteriorly.

**Distribution:** This species is known to occur from Mazatlan, Mexico, to Peru. Specimens dredged by the *Zaca* Expeditions were taken in depths from 7 to 40 fathoms.

***Arca (Cunearca) bifrons* Carpenter.**

*Arca brasiliiana* Lamarck, Reeve, Conch. Icon., Vol. 2, *Arca*, 1844, species 17, pl. 3, fig. 17. "San Blas, Bay of California (found on the sands); Cuming." [Not the record "Rio Janeiro, coast of Brazil"].

*Arca bifrons* Carpenter, Cat. Mazatlan Shells, February, 1856, p. 134. "Mazatlan," Mexico.

*Arca (Cunearca) bifrons* Carpenter, Maury, Palaeontogr. Amer., Vol. 1, No. 4, 1922, p. 197 (35), pl. 31 (3), fig. 12. Near the mouth of Rio Chepo, Panama.

**Type Locality:** Mazatlan, Mexico.

**Range:** Gulf of California, to Paita, Peru.

**Collecting Station:** Costa Rica: Gulf of Dulce.

**Description:** Shell with about 30 rather broad ribs on the left valve, the anterior ones transversely wrinkled, not nodulose, the posterior ones flat, subobsolete and separated only by very narrow interspaces.

A single left valve referred to *Arca bifrons* is present in the collection from the Gulf of Dulce, Costa Rica. It agrees with Reeve's figure (pl. 3, fig. 17) and with that given by Maury (pl. 31 (3), fig. 12). We are inclined to question the reference to Sowerby's figure (Gen. Shells, pl. 217, fig. 3) of *A. inaequilateralis* to *A. bifrons*. Apparently the name *bifrons* proposed by Carpenter has priority over the name *cordata* of Deshayes which was proposed for *A. cardiiformis* Sowerby, 1833, not *A. cardiiformis* Basterot, 1825.

The shell of *Arca bifrons* is larger and thicker than that of *A. aequatorialis*. It also differs from *Arca aequatorialis* in that the posterior end is less produced and the shell slopes more steeply from the posterior umbonal ridge.

***Arca (Cunearca) esmeralda* Pilsbry & Olsson.**

*Arca (Cunearca) esmeralda* Pilsbry & Olsson, Proc. Acad. Nat. Sci. Philadelphia, Vol. 93, September 9, 1941, p. 53, pl. 13, figs. 4 and 5. "Canoa formation, Punta Blanca," Ecuador, Pliocene.

**Type Locality:** Punta Blanca, Ecuador, Canoa formation, Pliocene.

**Range:** Isabel Island, Mexico, to Panama.

**Collecting Station:** Panama: Gulf of Chiriqui (221-D-1-5), 30-40 fathoms, sandy mud.

**Description:** Shell fairly large and moderately thick; valves ornamented by 26 to 28 ribs, those on the left valve strongly nodose, and on the right valve the anterior 8 or 10 are strongly nodose and the remainder are weakly nodose or smooth; a low wide depressed area extends from the beaks to the posterior ventral margin, most noticeable on large specimens; beaks strongly prosogyrate; the apex of the ligamental area is situated about a third of the length from the anterior end; the area is ornamented by 2 to 4 chevron-shaped grooves; hinge with a row of teeth which are a little larger at the ends than in the middle, there are about 18 to 20 teeth in the anterior series and 32 to 34 in the posterior series; the margins of the valves are fluted. The dimensions of the type specimen were given as: length, 57 mm., height, 53 mm., semi-diameter, 25.5 mm.

The shell of *Arca esmeralda* differs from those of the other West American species of *Cunearca* in that it possesses chevron-



shaped grooves on the ligamental area. Small shells of *Arca esmeralda* differ from those of *Arca nux* in that they have chevron-shaped grooves on the ligamental area which is less sloping, in the more numerous ribs, 26 to 28 rather than 22 to 23, the posterior dorsal area is more inflated and less steeply sloping and lacks the strong posterior umbonal angulation, and the posterior margin is more rounded. *Arca esmeralda* attains a much greater size than does *A. nux*.

Specimens dredged off Mexico and Panama agree so closely with the description and illustrations of *Arca esmeralda*, which was described from the Pliocene of Ecuador, that we have referred them to that species.

**Distribution:** This species occurs from off Isabel Island, Mexico, to Panama. It is also known to occur in the Pliocene of Ecuador.

#### *Arca (Cunearca) nux* Sowerby.

*Arca nux* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 19. "Hab. ad Xipixapi." "Found in sandy mud at a depth of twelve fathoms."—Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 1, pl. 1, fig. 1. Original locality record cited.

**Type Locality:** Xipixapi, Ecuador, in 12 fathoms, sandy mud.

**Range:** Concepcion Bay, Lower California, to Zorritos, Peru.

**Collecting Stations:** Mexico: Santa Inez Bay, Gulf of California (145-D-1 to 3), 4-13 fathoms, sand; Banderas Bay; Tenacatita Bay; Guatemala: 7 miles west of Champerico (197-D-1-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1-2), 13-14 fathoms; Meanguera Island, Gulf of Fonseca, 16 fathoms, sand, mud; Nicaragua: Corinto (200-D-10-11-19), 7-13 fathoms, mangrove leaves, sand; Costa Rica: Port Parker (203-D-1-3), 12-15 fathoms, sandy mud, crushed shell, shelly mud; Port Culebra (206-D-1-2-3), 14 fathoms, sandy mud; Golfito, Gulf of Dulce; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

**Description:** Shell small, oblique, gibbous, ornamented by about 22 to 23 ribs. Specimens of this species are usually not over 15 to 20 mm. in altitude and the ribs are often noded although sometimes only slightly so. The beaks are situated anteriorly about two-thirds to three-fourths the length of the hinge line and the ligamental area is asymmetrical.

In *Arca perlabiata* the beaks are nearly central and the ligamentary area is symmetrical. *Arca chemnitzii* Philippi from the Caribbean region is similar to *A. nux*, but has a thicker shell, steeper posterior slope and broader ligamentary area.

**Distribution:** This species occurs in fairly shallow water from the Gulf of California to Peru.

#### *Arca (Cunearca) perlabiata* Grant & Gale.

*Arca labiata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 21. "Hab. ad Real Llejoes et ad Tumbes." "Dredged among sandy mud at a depth of seven fathoms." Coll. Cuming.—Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1844, species 7, pl. 1, fig. 7. Original locality record cited.

*Scapharca (Cunearca) labiata* Sowerby, Maury, *Palaeontogr. Amer.*, Vol. 1, No. 4, 1922, p. 199 (37), pl. 29 (1), fig. 8. Peru.

*Arca (Arca) perlabiata* Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 141. Earlier records cited. New name for *Arca labiata* Sowerby, not *Arca labiata* Sölander.

**Type Locality:** Real Llejoes [near Corinto], Nicaragua, here designated. Tumbes, Peru, also cited originally.

**Range:** Magdalena Bay, Lower California, and the Gulf of California, to Tumbes, Peru.

**Collecting Stations:** Mexico: Arena Bank, Gulf of California (136-D-2), 45 fathoms, *Arca* conglomerates; Tangola-Tangola (196-D-17), 23 fathoms, mud; Nicaragua: Corinto; Isla Cardon; Costa Rica: Port Parker (D-1, 3), 12-15 fathoms, sandy mud, crushed shell, shelly mud; Ballena Bay, Gulf of Nicoya (213-D-11 to 17), 35 fathoms, mud.

**Description:** Shell heart-shaped, high and fairly thick. There are about 28 ribs which are transversely lightly nodulous. It bears considerable resemblance to *Arca nux* but can be separated by the heavier and much less oblique and larger shell, more numerous ribs, and in that the beak is nearly central in relation to the symmetrically diamond-shaped ligamentary area, while in *A. nux* the beaks are anterior and the area is asymmetrical.

*Arca chemnitzii* Philippi from the Caribbean has a smaller, less symmetrical ligamentary area and the beaks are anterior to the center of the shell rather than almost central as in *A. perlabiata*.

*Arca cacica* Olsson from the Miocene of Costa Rica is said to bear some resemblance to *A. nux*.

**Distribution:** This species occurs from Magdalena Bay, Lower California, and the Gulf of California, to Peru. It has been taken on sand bars at extreme low tide and has been dredged in rather shallow water. It is also known to occur in the Pleistocene of southern California and Lower California.

#### Subgenus *Larkinia* Reinhart.

##### KEY TO THE SPECIES OF *Larkinia*.

- A. About 25 to 27 radial ribs.....*grandis*  
B. About 31 to 38 radial ribs.....*multicostata*

#### *Arca (Larkinia) grandis* Broderip & Sowerby.

*Arca grandis* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, January, 1829, p. 365. "Hab."

—Reeve, Conch. Icon., Vol. 2, *Arca*, December, 1843, species 4, pl. 1, fig. 4. "Hab. Real Llejós, Bay of Guayaquil, etc., western coast of South America; Cuming, Hinds."

*Type Locality*: Original locality not known. Panama Bay here designated as type locality.

*Range*: Magdalena Bay, Lower California, and the Gulf of California, to Tumbes, Peru.

*Collecting Stations*: Nicaragua: Potosi and Monypenny Point; Castanones Peninsula, Corinto; Isla Encantada, Corinto; Costa Rica: Port Parker; Ballena Bay; Jasper Island; Golfito Bay; Panama: Bahia Honda.

*Description*: This is a large, very thick, squarish *Arca* which occurs commonly at Panama and other Central American localities and is used for food. These big shells are very thick and may weigh as much as two and one-half pounds. They are ornamented by about 25 to 27 radial ribs which may be slightly nodulous anteriorly.

The closest relatives of this species occur in the Miocene of the Caribbean region where a number of names have been applied to various forms such as *Arca patricia* Sowerby, *Arca usiacurii* Anderson, *Arca patriarcha* Anderson, *Arca patricia waringi* Maury, *Arca grandis colombiensis* Weisbord, and *Arca grandis cedralensis* Weisbord.

*Distribution*: This species occurs from Lower California to Peru. It is often taken at extreme low tide on sand bars.

#### *Arca (Larkinia) multicostata* Sowerby.

*Arca multicostata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 21. "Hab. ad oras Americae Centralis." "Dredged from a depth of twelve fathoms in the Gulf of Tehuantepec."—Reeve, Conch. Icon., Vol. 2, *Arca*, 1844, species 23, pl. 4, fig. 23. Original locality record cited.

*Type Locality*: Gulf of Tehuantepec, Mexico, in 12 fathoms.

*Range*: Newport Bay, California, to Panama, and the Galápagos Islands.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (141-D-1 to 4, and shore), 7-10 fathoms, sand, sandy mud, crushed shell, weed; Santa Inez Bay (145, shore); Santa Inez Bay, Monument Station; Cerralbo Island, Gulf of California; Arena Point, Lower California; Gorda Banks, Gulf of California (150-D-6), 60 fathoms, muddy sand, rocks; Chamela Bay; Tenacatita Bay; Port Guatulco; Tangola-Tangola (196-D-8), 9 fathoms, sand; Costa Rica: Port Parker; Culebra Bay.

*Description*: *Arca multicostata* Sowerby somewhat resembles *A. grandis* Broderip & Sowerby but is easily separated by the presence of about 31 to 36 ribs rather than about 25 to 27 in *A. grandis* which species

has a much heavier shell. *Arca (Anadara) reinharti* Lowe is somewhat similar to small shells of *Arca multicostata* but it has only about 25 to 27 radiating ribs and is a much more oblique shell. Both *Arca reinharti* and young specimens of *A. multicostata* are slightly inequivalved, the left valve overlapping the right.

*Distribution*: This species occurs from southern California to Panama and the Galápagos Islands. In tropical waters it is occasionally taken on sand bars at very low tide and may be dredged in shallow waters.

#### Subgenus *Scapharca* Gray.

##### KEY TO THE SPECIES OF *Scapharca*.

- A. Shell with 39 or more ribs.....*obesa*
- B. Shell with about 30 to 32 ribs
  - a. Shell elongate, anterior ribs grooved.....*concinna*
  - aa. Shell squarely ovate, anterior ribs not grooved.....*cepoides*

#### *Arca (Scapharca) cepoides* Reeve.

*Arca cepoides* Reeve, Conch. Icon., Vol. 2, March, 1844, species 66, plate 10, fig. 66. "Hab. San Miguel, South America (found in sandy mud); Cuming."

*Type Locality*: San Miguel, Panama, in sandy mud.

*Range*: Cerralbo Island, Gulf of California, to San Miguel, Panama.

*Collecting Station*: Mexico: Cerralbo Channel, Gulf of California (137-D-3), 46 fathoms, rock.

*Description*: Shell rather large, subquadrate, ventricose, ornamented by about 32 smooth flat-topped ribs. The specimens obtained in the present collection are small, less than 15 mm. in length.

*Distribution*: This species is rather rarely taken but is known to occur from the Gulf of California to Panama.

#### *Arca (Scapharca) concinna* Sowerby.

*Arca concinna* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 20. "Hab. in America Centrali." "Found in coarse sand, at a depth of twelve fathoms, in the Gulf of Nocoioy."—Reeve, Conch. Icon., Vol. 2, *Arca*, 1844, species 34, pl. 6, fig. 34. Original locality record cited.

*Type Locality*: Gulf of Nicoya, Costa Rica, in 12 fathoms, coarse sand.

*Range*: Santa Inez Bay, Lower California, to Panama.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (143-D-4-5), 18-25 fathoms, sand; Arena Bank, Gulf of California (136-D-2), 45 fathoms, mud, *Arca* conglomerates; 4 miles south-southwest of Maldonado Point (192-D-1,-3), 26-38 fathoms, mud; Tangola-Tangola Bay (196-D-1,-18-19-20), 5-50 fathoms, gray sand, mud;

Costa Rica: Cedro Island, Gulf of Nicoya (213-D-1, 10), 10 fathoms, mud; off Ballena Bay, Gulf of Nicoya (213-D-11, 17), 35 fathoms, mud; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description:* Shell elongate, and ornamented by about 30 rather fine ribs, of which the most anterior ones are divided by a medial groove.

This shell resembles in general characters *A. inaequilateralis* Guppy from the Miocene of the Caribbean region.

*Distribution:* This species is known to occur at various localities from the Gulf of California to Panama. Most of the specimens dredged by the *Zaca* Expeditions were from depths of 18 to 50 fathoms.

#### *Arca (Scapharca) obesa* Sowerby.

*Arca obesa* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 21. "Hab. in Columbia Occidentali." "A few specimens only were dredged, in seven fathoms, at Atacamas."—Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1843, species 3, pl. 1, fig. 3. Original locality cited.

*Type Locality:* Atacamas, Ecuador, in 7 fathoms.

*Range:* Off San Jose del Cabo, Lower California, Mexico, to Negritos, Peru.

*Collecting Stations:* Mexico: Tangola-Tangola (196-D-17), 23 fathoms, mud; Guatemala: 7 miles west of Champerico (197-D-1-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1-2), 13-14 fathoms, mud; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves on bottom; Costa Rica: 14 miles southeast of Judas Point (214-D-4), 61 fathoms, mud, rocks; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description:* The ventricose ovate form and large number of fine, close-set ribs are characteristic of *Arca obesa*. The species usually has about 42 to 44 ribs but some specimens from La Libertad, El Salvador, have only 39.

*Distribution:* This species occurs from Lower California to Peru but is not a common species. The specimens from the *Zaca* Expeditions were dredged from depths of 12 to 61 fathoms.

#### GENUS *Noetia* GRAY.

##### Subgenus *Noetia* s.s.

*Noetia (Noetia) reversa* Gray in Sowerby.

*Arca reversa* Gray (MS) in Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 20. "Hab. in Peruvia." "Found in soft mud, at a depth of seven fathoms, at Tumbes."—Reeve, *Conch. Icon.*, Vol. 2, *Arca*, 1843, species 5, pl. 1, fig. 5. Original locality record cited.

*Type Locality:* Tumbes, Peru, in 7 fathoms, soft mud.

*Range:* Gulf of California, to Peru.

*Collecting Stations:* Guatemala: 7 miles west of Champerico (197-D-1-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1-2), 13-14 fathoms, mud; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves on bottom; Isla Cardon, Corinto; Costa Rica: Golfito, Gulf of Dulce; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description:* Shell of medium size, sub-trigonal, inflated, equivalve, ornamented by about 36 ribs. Anterior end rounded, posterior end sloping and subtruncated. Beaks large, prominent, posterior, and curved toward the posterior of the shell.

*Distribution:* This species occurs at various localities from the Gulf of California to Peru. Specimens collected by the *Zaca* Expeditions were dredged at depths of 12 to 40 fathoms.

##### Subgenus *Sheldonella* Maury.

##### *Noetia (Sheldonella) delgada* Lowe.

*Arca delgada* Lowe, *Trans. San Diego Soc. Nat. Hist.*, Vol. 8, No. 6, March 21, 1935, p. 16, pl. 1, fig. 2. "Manzanillo, 20 fathoms."—MacNeil, *U.S. Geol. Surv., Prof. Paper* 189-A, 1938, p. 39. Original record cited.

*Type Locality:* Manzanillo, Mexico, 20 fathoms.

*Range:* Manzanillo, Mexico.

*Collecting Station:* Mexico: Manzanillo (184-D-2), 30 fathoms, gravelly sand.

*Description:* Shell ornamented by about 30 ribs. The rounded posterior portion of the shell is expanded and very obliquely produced.

MacNeil has suggested the possibility that *Arca delgada* may be related to *Noetia (Eontia) centrota* Guppy which has been reported from the upper Miocene and Pliocene of Trinidad. However, the general shape of *delgada* appears to be closer to that of *Noetia (Sheldonella) maoica* Maury from the Miocene of the Dominican Republic.

*Distribution:* This species is known only from the type locality, Manzanillo, Mexico, where it has been dredged in 20 to 30 fathoms.

##### Subgenus *Eontia* MacNeil.

##### *Noetia (Eontia) olssoni* Sheldon & Maury.

*Noetia olssoni* Sheldon & Maury, *Palaeontogr. Amer.*, Vol. 1, No. 4, 1922, p. 172 (10), pl. 29 (1), figs. 6, 9 (as *Arca (Noetia) olssoni* on expl. to plate). "Bucaru," Los Santos Province, Panama.

*Eontia olssoni* Sheldon & Maury, MacNeil, *U. S. Geol. Surv., Prof. Paper* 189-A, 1938, p. 13, pl. 1, figs. 19, 20. Earlier records cited.

*Type Locality:* Bucaru, port of Tonosi, Los Santos Province, Panama.

**Range:** Corinto, Nicaragua, to Negritos, Peru.

**Collecting Station:** Nicaragua: Corinto (200-D-10, 11, 19), 7-13 fathoms, mangrove leaves, sand.

**Description:** The shell of *Noetia* (*Eontia*) *olssoni* is easily recognized from that of other west American species of *Noetia* by the narrow, elongate shell in which the posterior end is not transversely expanded but bears a medial depression.

*Noetia olssoni* is similar to *N. centrota* Guppy from the upper Miocene and Pliocene of Trinidad, and *N. bisulcata* Lamarck, Recent in the Caribbean and Atlantic coast of South America from Colombia to Uruguay. The west American species differs in the greater length posteriorly, more central beaks and nearly equal rows of teeth and in other details. The largest specimen in the present collection measures 14.6 mm. in length.

**Distribution:** The occurrence of this species at Corinto, Nicaragua, furnishes an extension northward in its range. It occurs south to Peru. It is also known to occur in the Pleistocene of Magdalena Bay, Lower California.

## Superfamily Pteriacea.

### Family Pteriidae.

#### KEY TO THE GENERA OF THE PTERIIDAE.

- A. Hinge extended posteriorly forming a wing ..... *Pteria*  
 B. Hinge not extended posteriorly to form a wing ..... *Pinctada*

#### GENUS *Pteria* SCOPOLI.

##### *Pteria sterna* Gould.

*Avicula sterna* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 93. "Inhabits Mazatlan."—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, 1853, p. 404, pl. 16, fig. 7. "Inhabits Mazatlan? Lieut. Green. Panama. Prof. Adams, Col. Jewett."

*Avicula peruviana* Reeve, *Conch. Icon.*, Vol. 10, *Avicula*, March, 1857, species 53, pl. 14, fig. 53. "Hab. Peru."

**Type Locality:** Mazatlan, Mexico.

**Range:** Hueneme Point, California, to the Gulf of California, and south to Paita, Peru.

**Collecting Stations:** Mexico: Cedros Island, in channel (126-D-19), 25 fathoms, rocks, algae; Santa Inez Bay: Arena Bank; Cape San Lucas, Lower California.

**Description:** Shell oblique and with a posterior wing and shorter anterior ear beneath which is a byssal notch. Rows of spines occur on unworn shells. On worn shells yellowish stripes usually are present on a brown background.

The degree of development of a posterior wing, thickness of shell, and obliquity of

the hinge line appear to be variable characters in *Pteria sterna*. Some specimens have a well developed posterior wing while in others this is only slightly developed. In some specimens it can be observed that a long wing was present in the young stage but later the sinus on the posterior margin became more rounded and thus produced only a small wing. Some specimens possess thicker shells of a dark color which are ornamented by fine radial color bands. This appears to be an inconstant character as shown by some specimens on which the earlier part of the shell is dark and the later part is ornamented by yellowish stripes. Odhner pointed out that the width of color bands of *Pteria* (*Electrotoma*) *zebra* Reeve depends upon the situs to which it is attached.

From a consideration of the characters shown in a series of specimens it appears that there is no satisfactory basis for separating *Pteria peruviana* Reeve from *P. sterna* Gould.

**Distribution:** This species occurs at various localities from southern California to Peru. It is only occasionally found in southern California, but it occurs rather abundantly at certain localities in the Gulf of California. It does not occur in the great numbers originally found in the Gulf of California due to pearl fishing. This species is said to have produced literally bushels of pearls.

#### GENUS *Pinctada* BOLTON.

##### *Pinctada mazatlanica* Hanley.

*Meleagrina mazatlanica* Hanley, *Cat. Rec. Bivalve Shells*, Ap., 1856, p. 388, pl. 24, fig. 40. "Mazatlan."

*Avicula barbata* Reeve, *Conch. Icon.*, Vol. 10, *Avicula*, March, 1857, species 9, pl. 5, fig. 9. "Hab. Panama (under stones at low water); Cuming."

**Type Locality:** Mazatlan, Mexico.

**Range:** Gulf of California, to Paita, Peru, and the Galápagos Islands.

**Collecting Stations:** Mexico: Santa Inez Bay, near Concepcion Point, Lower California; Banderas Bay; Chamela Bay; Passavera Island, Chamela Bay (shore); Port Guatulco (195-D-15, also shore), 1.5 fathoms, coral bottom; Tangola-Tangola Bay; Nicaragua: Isla Cardon, Corinto; Costa Rica: Port Parker; Potrero Grande; Culebra Bay; Golfito, Gulf of Dulce; Piedra Blanca; Colombia: Gorgona Island.

**Description:** This is the "concha de perla" or "Panama shell," the common commercial pearl oyster of the Gulf of California and Panama. The color of the exterior of the shell of *Pinctada mazatlanica* is grayish-yellow or light brown. On unworn specimens there are radial rows of pointed foliaceous spines and often radial rows of

spots a little darker than the ground-color. The nacre is silvery white with a narrow golden or brassy colored margin.

This species is closely related to *Pinctada margaritifera* Linnaeus, one of the well known pearl oysters of the Indo-Pacific region. Jameson believed that there is intergradation between the two species. He also mentioned that in the group related to *P. margaritifera*, the lightest colored forms, *mazatlanica*, *zanzibarensis*, *persica* and *erythraensis*, occur on the shores of the great continents, the Australian and Malay shells are intermediate in color, and the oceanic variety *cumingii* is darkest in color.

Compared to *Pinctada margaritifera* and others of the group, *P. mazatlanica* is characterized by its greater convexity, greater anterior projection, and light brown color. Jameson pointed out that the anterior margin below the byssal notch projects farther forward than in any other related form. A perpendicular to the anterior end of the hinge would cut off about one-third of the valve. The posterior angle of *mazatlanica* is acute or but rarely a right angle. The posterior margin of the nacre slopes forward from the hinge, resembling in this character *P. maxima* Jameson described from New Guinea.

**Distribution:** This species occurs from the Gulf of California to Peru. It is fairly abundant at various localities in the Gulf of California and Panama where it is fished for pearls. It was formerly very abundant in the Gulf of California but the beds have been greatly depleted due to pearl fishing.

### Family Pinnidae.

#### KEY TO THE GENERA OF THE PINNIDAE.

- A. Shell triangular; a median groove interiorly dividing the nacreous layer into two parts.....*Pinna*
- B. Shell ham-shaped; no median groove interiorly.....*Atrina*

#### GENUS *Pinna* LINNAEUS.

##### *Pinna rugosa* Sowerby.

*Pinna rugosa* Sowerby, *Proc. Zool. Soc. London*, September 25, 1835, p. 84. "Hab. in Sinu Panamensi. (Isle of Rey)." "They were procured from sand banks."—Reeve, *Conch. Icon.*, Vol. 11, *Pinna*, 1858, species 50, pl. 26, fig. 50. Original locality cited.

**Type Locality:** Isle of Rey, Bay of Panama, sand banks.

**Range:** Manuela Lagoon, Lower California, and Punta Penasco, Sonora, Mexico, to Panama.

**Collecting Stations:** Mexico: Gorda Banks, Gulf of California (150-D-7), rock, calcareous algae; Acapulco; Nicaragua: Corinto (200-D-1-3), 2—6.5 fathoms, man-

grove leaves; Castanones Peninsular Lagoon, Corinto; Costa Rica: Long Beach N. W. of Port Parker; Golfito Bay; Gulf of Dulce.

**Description:** This species possesses an elongate, triangular, rugose shell. It grows to a length of a foot and a half or more and is ornamented by about eight rows of foliaceous, tubular spines. The spines may be almost obsolete on old specimens.

**Distribution:** This species occurs rather commonly along the west coast of Mexico and south to Panama.

#### GENUS *Atrina* GRAY.

##### KEY TO THE SPECIES OF *Atrina*.

- A. Shell ornamented by 26-38 rows of spines
  - a. About 38 rows of spines; ventral margin broadly rounded.....*oldroydii*
  - aa. About 26 rows of spines; ventral margin slightly rounded.....*texta*
- B. Shell ornamented by about 18 rows of strong, regular, tubular spines.....*maura*

##### *Atrina maura* Sowerby.

*Pinna maura* Sowerby, *Proc. Zool. Soc. London*, September 25, 1835, p. 84. "Hab. apud Panamam." Obtained "from muddy banks."—Reeve, *Conch. Icon.*, Vol. 11, *Pinna*, 1858, species 54, pl. 29, fig. 54. Original locality cited.

**Type Locality:** Panama, muddy banks.

**Range:** Santo Domingo (in kitchen middens), and Magdalena Bay, Lower California, and Punta Penasco, Sonora, Mexico, to Peru.

**Collecting Stations:** Mexico: Gulf of California, Santa Inez Bay, near Point Concepcion along shore of Lower California, also at Monument Station; Banderas Bay; Nicaragua: Monypenny Point, Gulf of Fonseca, 4 fathoms, mud; Corinto (200-D-1-10), 1/2 to 7 fathoms, mangrove leaves.

**Description:** The shell of this species has a nearly straight dorsal margin. About 18 rows of fairly strong, unusually regular, yellowish-white arched tubular spines occur on a brown or rusty black background; these spines almost disappear on the anterior side. Some specimens are of a yellowish or dark greenish-olive color.

According to Pilsbry and Lowe the shells of *Atrina maura* are known as "hachas" or hatchets by the native fishermen along western Mexico. The large white muscle which is used for food is said to resemble and taste much like that of the giant scallop of the Atlantic Coast.

Winckworth indicated that "*Pinna*" *tuberculosa* Sowerby is identical with "*Pinna*" *maura* Sowerby. However, the descriptions of Sowerby and Hanley and the figures given by Reeve seem to indicate that *tuber-*

*culosa* is a distinct species and that *Pinna lanceolata* Sowerby, a preoccupied name, can be placed in the synonymy of *maura*. The shell of *Atrina tuberculosa* Sowerby is triangular, inflated, and quite different in general appearance from that of *A. maura*.

*Atrina rigida* Dillwyn from the Antillean region bears a resemblance to *A. maura*.

***Atrina oldroydii* Dall.**

*Atrina oldroydii* Dall, *Nautilus*, Vol. 14, No. 12, April, 1901, p. 143. "Taken alive by fishermen in 25 fathoms, San Pedro Bay," California.—Dall, *U. S. Nat. Mus., Bull.* 112, 1921, p. 17, pl. 2, figs. 4, 5, 6. Off San Pedro, California, in 25 fathoms.

*Type Locality*: San Pedro Bay, California, in 25 fathoms.

*Range*: San Pedro, California, to Cedros Island, and Magdalena Bay, Lower California.

*Collecting Station*: Mexico: east of Cedros Island, in Channel (126-D-17), 40 fathoms, mud.

*Description*: The shell of this large dark colored *Atrina* from southern California and Lower California is much wider than that of *Atrina texta* n. sp. and the posterior end is more oblique and less square in outline than is that of *A. maura*. There are about 38 radiating ribs which bear rather fine low spines which do not extend over the ventral surface and on the posterior fourth of the shell the ribs and spines are obsolete. The specimens in the present collection are broken but the largest one measures 240 mm. from beak to base.

*Atrina serrata* Sowerby from the Atlantic coast is a similar species.

*Distribution*: This species is not commonly found but is known to occur in the waters off southern California and along the west coast of Lower California, south to Magdalena Bay.

***Atrina texta* Hertlein, Hanna & Strong,  
sp. nov.**

Plate I, Figures 9 and 10.

Shell roughly triangular with a curved beak; dorsal side gently convex, the ventral concave behind the beak then gently convex, straightening out to the posterior margin which is gently rounded; shell translucent, showing the external sculpture on the interior; color pale horn brown, darker on the beaks and on a large irregular blotch over the muscle scar; posterior margins gaping about 10 mm. and ventral margin gaping about 5 mm. in the concave portion behind the beaks; exterior sculpture consisting of about 26 radial rows of short and low triangular spines, slightly recurved; these spines are also regularly arranged in rows concentric with the growth lines; this zone of sculpture completely crosses the

ventral margin but the rows become fewer anteriorly as the zone crosses the umbonal ridge; ventral zone marked only by rather coarse growth lines except posteriorly where the radial rows of spines gradually fade away. Length, 141 mm.; width, 80 mm.; convexity, 35 mm.

Holotype in Calif. Acad. Sci. Paleo. Type Coll., from Sta. 150-D-4, Gorda Bank area off the southern end of Lower California, Lat. 23°01' N., Long. 109°30' W.; dredged in 70 fathoms; collected by the Templeton Crocker-Beebe Expedition, April 21, 1936.

This interesting species has been compared with all the other west coast forms of *Atrina* and in none of them is there found the combination of characters shown here. *Atrina oldroydii* Dall is perhaps the closest; that species also has radial and concentric rows of fine spines but the shape is decidedly asymmetrical, the beaks are not hooked and the dorsal margin is scarcely convex. The shell of the new species differs from that of *Atrina maura* Sowerby in the wider, squarer posterior end and in that it is ornamented by about 26 radial rows of triangular spines rather than about 18 rows of regular, semitubular spines.

**Family Pedalionidae.**

**GENUS *Pedalion* SOLANDER IN HUDDSFORD.**

***Pedalion chemnitzianum* d'Orbigny.**

Plate I, Figure 8.

*Perna chemnitziana* d'Orbigny, in Sagra, *Moll. Cuba*, Vol. 2, 1845, p. 346. "Nous l'avons reçue de Cuba, de la Martinique et de Sainte-Croix; elle vit attachée aux rochers par son byssus au niveau des basses marées ordinaires." Reference to *Concha semiaurita* Chemnitz (not *Ostrea semiaurita* Linnaeus), *Neues Syst. Conchyl.-Cab.*, Vol. 7, p. 250, Tab. 59, fig. 580. West Indies.

*Type Locality*: Cuba, here designated. Martinique and St. Croix also cited originally.

*Range*: Coronado Islands, off the west coast of northern Lower California, Mexico, to Chile. Also Atlantic.

*Collecting Stations*: Mexico: Sulphur Bay, Clarion Island; Port Guatulco (195-D-14), 4 fathoms, coral; also on shore; Tangola-Tangola, on beach; Nicaragua: Fumarole Island; Potosi and Monypenny Point; Costa Rica: Piedra Blanca.

*Description*: The shell of *Pedalion chemnitzianum* is very variable. It may be quadrate, elongate, or irregular in shape and it may be fairly thick or thin. It is sometimes ornamented by fine radial ornamentation but usually this is lacking and the exterior shows only scaly concentric layers. The color may be yellowish-brown but often it is partially and occasionally almost wholly, of a purple color. There are usually about 6

to 8 and occasionally as many as 12 ligamental pits along the hinge line. Right valve with a byssal sinus.

There appears to be no satisfactory method of separating the west American forms here referred to *Pedalion chemnitzianum* from the east American species of this name. Many workers familiar with the Atlantic species have been unable to detect any constant differences between the forms occurring on the east and west coast. *Pedalion janus* Carpenter, a species occurring commonly from San Ignacio Lagoon, Lower California, and the Gulf of California to Oaxaca, Mexico, usually possesses a thinner shell ornamented by radial sculpture, and it

apparently has a more northern distribution; at least it has not been observed by us in collections from Panamic waters. However some specimens seem to show the characters of both *P. chemnitzianum* and *P. janus*, as pointed out by Stearns. No doubt the two forms are closely related. Carpenter believed that variants of *P. chemnitzianum* approach the Hawaiian species *P. incisum* Conrad, while those of *P. janus* approach *P. costellatum* Conrad.

*Distribution*: This species occurs commonly attached to rocks or other objects between tides or in shallow water from northern Lower California to Chile, and also Florida and the Caribbean region.



## EXPLANATION OF THE PLATE.

## PLATE I.

- Fig. 1. *Arca (Anadara) mazatlanica* Hertlein & Strong, sp. nov. Holotype, right valve, from Station 153-D-2, dredged in 120 fathoms (218 meters), Lat.  $23^{\circ}06'00''$  N., Long.  $106^{\circ}47'00''$  W., 19 miles west of Mazatlan, Sinaloa, Mexico. Length, 62 mm., height, 36.3 mm., convexity (one valve), 15.5 mm. P. 156.
- Fig. 2. *Arca (Anadara) similis* C. B. Adams. Hypotype, right valve, from Puntarenas Lagoon, Costa Rica. Length, 50 mm., height, 31.8 mm., convexity (one valve), 15mm. P. 157.
- Fig. 3. *Arca (Anadara) biangulata* Sowerby. Hypotype, left valve, from Station 143-D-5, dredged in 18 fathoms (33 meters), Lat.  $26^{\circ}54'00''$  N., Long.  $111^{\circ}53'00''$  W., Santa Inez Bay, Lower California. Length, 49 mm., height, 36 mm., convexity (one valve), 17 mm. P. 155.
- Fig. 4. *Arca (Anadara) mazatlanica* Hertlein & Strong, sp. nov. Holotype. View of the interior of the left valve of the specimen shown in Fig. 1.
- Fig. 5. *Arca (Anadara) similis* C. B. Adams. View of the interior showing hinge of the left valve of the specimen shown in Fig. 2.
- Fig. 6. *Arca (Lunarca) vespertina* Mörch. Hypotype, right valve, from Loc. 27230

(C.A.S.), Petatlan Bay, about 6 miles south of Sihuatenejo, Guerrero, Mexico. View of the interior. Length, 36.1 mm., height, 22.5 mm., convexity (one valve), 9.1 mm. P. 158.

- Fig. 7. *Arca (Lunarca) vespertina* Mörch. View of the exterior of the specimen shown in Fig. 6.

The shell of this species becomes more elongate in large specimens such as this one, but juvenile forms are more quadrate in shape.

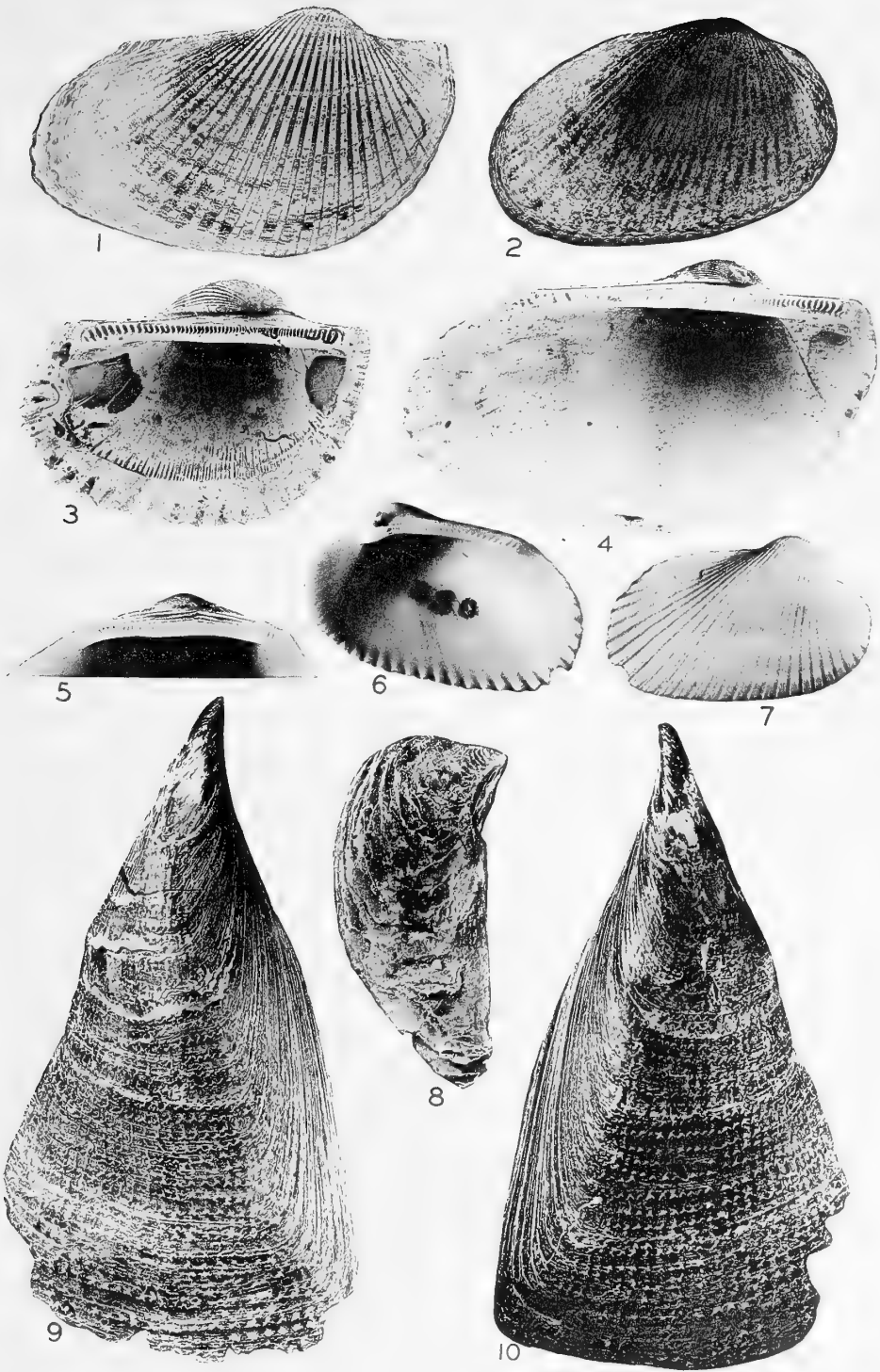
- Fig. 8. *Pedalion chemnitzianum* d'Orbigny. Hypotype, right valve, from Loc. 28186 (C.A.S.), Kino Bay, Sonora, Mexico. Length, 20.5 mm., height, 46.5 mm., convexity (both valves), 8 mm. P. 166.

- Fig. 9. *Atrina texta* Hertlein, Hanna & Strong, sp. nov. Holotype, right valve, from Station 150-D-4, Gorda Banks off the southern end of Lower California, Lat.  $23^{\circ}01'00''$  N., Long.  $109^{\circ}29'00''$  W., dredged in 70 fathoms (128 meters). Length, 141 mm., width, 80 mm., convexity (both valves), 35 mm. P. 166.

- Fig. 10. *Atrina texta* Hertlein, Hanna & Strong, sp. nov. Left valve of the specimen shown in Fig. 9.

All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.





MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA.



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## 20.

## Chemical Sensory Reactions in the Mexican Blind Characins.

C. M. BREDER, JR.

&amp;

PRISCILLA RASQUIN\*

*New York Zoological Society*

(Plates I-III; Text-figures 1-9).

## INTRODUCTION.

In the attempt to understand more fully the various features of the behavior and possible evolution in progressive stages of the changes in the Mexican blind fish of the *Astyanax mexicanus* (Philippi)—*Anoptichthys jordani* Hubbs and Innes series it is, of course, necessary to obtain some evaluation of the various sensory systems. The present contribution is therefore such an attempt to analyze the differences, if any such be present, in the chemical sensory equipment of these fishes. Both the structural and behavioristic elements involved are herewith discussed.

Recently a new form has been discovered in another cave by one of Dr. Hubb's collectors, as noted by Tafall (1942 and 1943) and Breder (1943). This form is evidently still further advanced in eye and pigmentation loss. We have been fortunate in obtaining some of these alive through the good offices of Mr. B. Dontzin who visited this cave, Cueva de los Sabinos, in 1942 for that express purpose. Tafall (1943) has made an important contribution to the ecology of both La Cueva Chica and Cueva de los Sabinos. In his study of conditions he enumerates the species of aquatic organisms and discusses at length the fishes of these caves, making comparisons with the fauna of the cenotes of Yucatan. The taxonomic considerations involved are under study by Dr. Hubbs, while the present paper discusses some of the anatomical and behavioristic items of this form compared with fishes from La Cueva Chica and normal-eyed river fishes. The details of the ocular anatomy and reactions to light in this form are discussed by Breder and Gresser (Ms.) A popular version of the history of these studies may be found in Bridges (1940 and 1943).

As in all studies concerned with the chemical senses of fishes it was found much more difficult to obtain definitive results than in the earlier studies on reactions to light of Breder and Gresser (194a and b). We feel, however, that enough data have been accumulated to indicate the basic nature of these features in reference to the behavior of the forms involved and the apparent nature of the evolutionary changes in progress.

The work was carried on in the Department of Animal Behavior of the American Museum of Natural History. We are grateful to Miss Annette Bacon for advice in connection with the mathematical treatment and for editorial assistance and to Lt. James W. Atz for numerous helpful comments.

## THE NASAL CAPSULE.

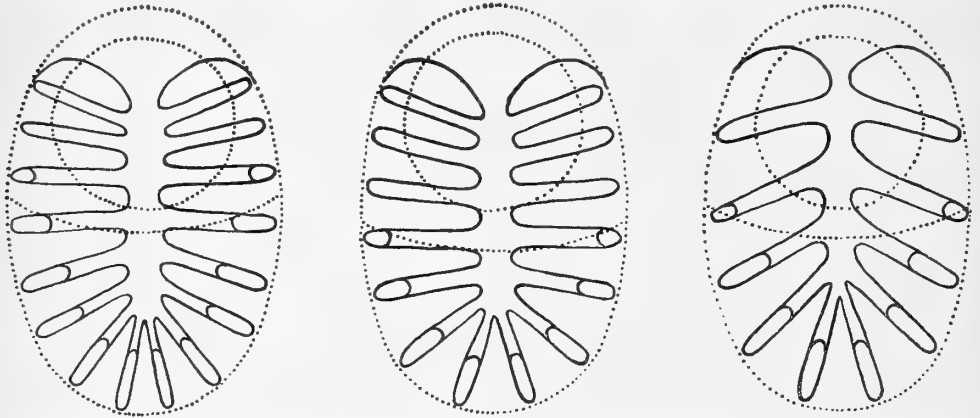
Serial sections and gross dissections of the nasal capsule of each of three types under comparison showed that these were rather typical characin structures, but that each form showed a slight but significant morphological difference, in which La Cueva Chica material was intermediate between the eyed river fish from the Rio Tampaon and Cueva de los Sabinos specimens. These differences were chiefly in the reduction of the number of sensitive lamellae and a decrease in the depth of the pit, proceeding from the river to the Cueva de los Sabinos stocks. The functional significance of the sense of smell involved in these changes is not entirely clear on an anatomical basis. The funnel-like flap that serves to direct water into the anterior opening increases in size slightly in this series as is indicated in Plate I, wherein the right hand flaps are shown in profile.

No histological difference could be found in the olfactory epithelium from one form to another. Text-figure 1 shows a conventionalized reconstruction of the ridges in relation to the positions of the anterior and

\* The studies embodied in this paper were started as part of the work in the graduate course in ichthyology given by the senior author at New York University. Subsequently the studies were expanded to their present form.

posterior nares of each type. As is indicated, in the river fish there are eight pairs of ridges, in La Cueva Chica material seven and in the Cueva de los Sabinos only five. A selected, approximately homologous section of each of these is shown photographically in Plate II. Here the raising of the floor of the pit and the more fully exposed positions of the finger-like lamellae sections in the Cueva de los Sabinos fish is indicated. It is also evident from this plate that in the river fish some of these lamellae become anchored at their distal ends more anteriorly and are more numerous than in either cave fish. The nasal openings of the Cueva de los Sabinos fish are larger and offer more direct exposure of the ridges to the exterior.

*vulgaris* Cuvier to number about ten pairs, figures the nasal pits of *Gadus morrhua* Linnaeus and *Mugil chelo* Linnaeus and discusses nasal anatomy in general. Adrian and Ludwig (1938) indicate about 31 pairs for *Ameiurus nebulosus*. Busnita (1932) discusses the histological details of the sensitive epithelium of *Carassius*, while Laibach (1937) shows that in development the nasal lamellae increase in number from four to thirty-six pairs as *Anguilla vulgaris* Linnaeus transforms from the leptocephalus stage and grows to adult size. That possible size or age difference could not have anything to do with the differential counts in the characins has been checked. Specimens long before reaching the size of a small adult



TEXT-FIG. 1. Diagrammatic representation of the sensory ridges in the nasal capsules of Mexican characins. Left: from Rio Tampaon, Middle: from La Cueva Chica. Right: from Cueva de los Sabinos. Based on reconstruction from serial sections and gross dissections. In each case the left nostril is represented in plan view with the fish facing upward. The dotted outlines represent the anterior and posterior external openings. See also Plates I and II.

Whether these features are to be interpreted as a reduction of nasal acuity, on the basis of a reduction of sensitive areas, or an increase, based on the greater exposure of the remaining areas and a larger funneling flap, is something that must wait on the availability of a larger stock of the Cueva de los Sabinos fish suitable for a more extended experimental analysis.

There is considerable variation in the nasal anatomy of teleosts as is well indicated by Liermann (1933) who figures the lamellar construction of *Carassius carassius* Nordmann, *Anguilla vulgaris* Flemming, *Perca fluviatilis* Linnaeus, *Pleuronectes flesus* Linnaeus, *Ammodytes tobianus* Linnaeus, *Zoarces viviparus* Linnaeus, *Gasterosteus aculeatus* Linnaeus and *Syphonostomum typhle* Linnaeus. Tretjakoff (1930) shows the lamellae of *Scomber scombrus* Linnaeus to be practically radially arranged and the platelets to number about twenty. Matthes (1934) shows the lamellae of *Tinca*

show a fixed and constant number. If such changes take place with the development of these characins it must be at a size below which we have comparative material. As would be expected the nasal capsules of the cyprinids more closely resemble those under discussion than do the other species more remotely related.

Many other authors have described the nasal anatomy of a variety of fishes including figures of *Zeus faber* Linnaeus and *Gadus morrhua* by Berghe (1929), *Protoperus* by Fullerton (1933) and various Heterosomata by Chabanaud (1927 and 1936). Derscheid (1924) discusses at length the nasal capsules of the Isospondyli with figures of the anatomy of no less than thirty species well distributed throughout the order. Most of these have numbers of lamellae much higher than our characins but the following approach them in this sense: *Chauliodus sloani* Bloch and Schneider with five, *Pantodon bucholtzi* Peters with ten



pairs, *Heterotis niloticus* Cuvier and Valenciennes with sixteen radially arranged, while seven species of Mormyridae of the genera *Marcusenius*, *Mormyrus*, *Genyomys* and *Mormyrops* range from six to eight pairs of lamellae. In general terms these Isospondyle nasal pits resemble those of the Ostariophysi about as closely as these two orders resemble each other in most respects. Frisch (1941a) indicates ten pairs of lamellae in the nasal pit of *Phoxinus laevis* Agassiz. It is evident from this brief survey of the literature, moreover, that the sensitive lamellae of these characins approach the lower limits in number much closer than they do the upper. From this and general considerations we cannot but conclude that the fishes in question are not nearly as well provided for in regard to olfaction as are many other species, including a number with especially well developed eyes.

### THE TASTE BUDS.

Complete serial sections of one of each of the three forms has made possible the reconstruction of the distribution of the taste bud tracts on the exterior surfaces of the fishes. The distribution of these in each is indicated in Text-figure 2. As each sectioned fish varied slightly in bodily proportions, all have been reduced to a standard outline in order to facilitate comparison. The actual outline of each fish is indicated by the small inserts. The dots on the surface of the outline are indicative of the positions of gustatory areas and are not intended to represent individual taste buds in terms of absolute number. It is clear from this figure that there is a marked increase in the areas of gustation from the river fish to those from Cueva de los Sabinos. This is the first unequivocal positive change that has been found in this series. Other changes found, excepting perhaps only the nasal pits, have all been in the nature of reductions, Breder and Gresser (1941a) and Breder (1943). It is to be noted in this figure that the optic area in La Cueva Chica stock, 7th generation of aquarium-reared fishes, is scarcely encroached upon by taste buds whereas in the more advanced Cueva de los Sabinos material this area is well covered by them. The former had a sunken eye, uncovered, lacking a lens and similar to the fish of Plate II of Breder and Gresser (1941a). While the general form of the chief tracts of taste buds is fairly constant it is to be noted that with the increasing number there is evidently some slight translocation of some of the areas of taste. Also, along with this increase in taste areas, chiefly on the head, there is evidently some slight reduction of them on the caudal fin, but this is perhaps little more than a matter of individual variation. These findings have been

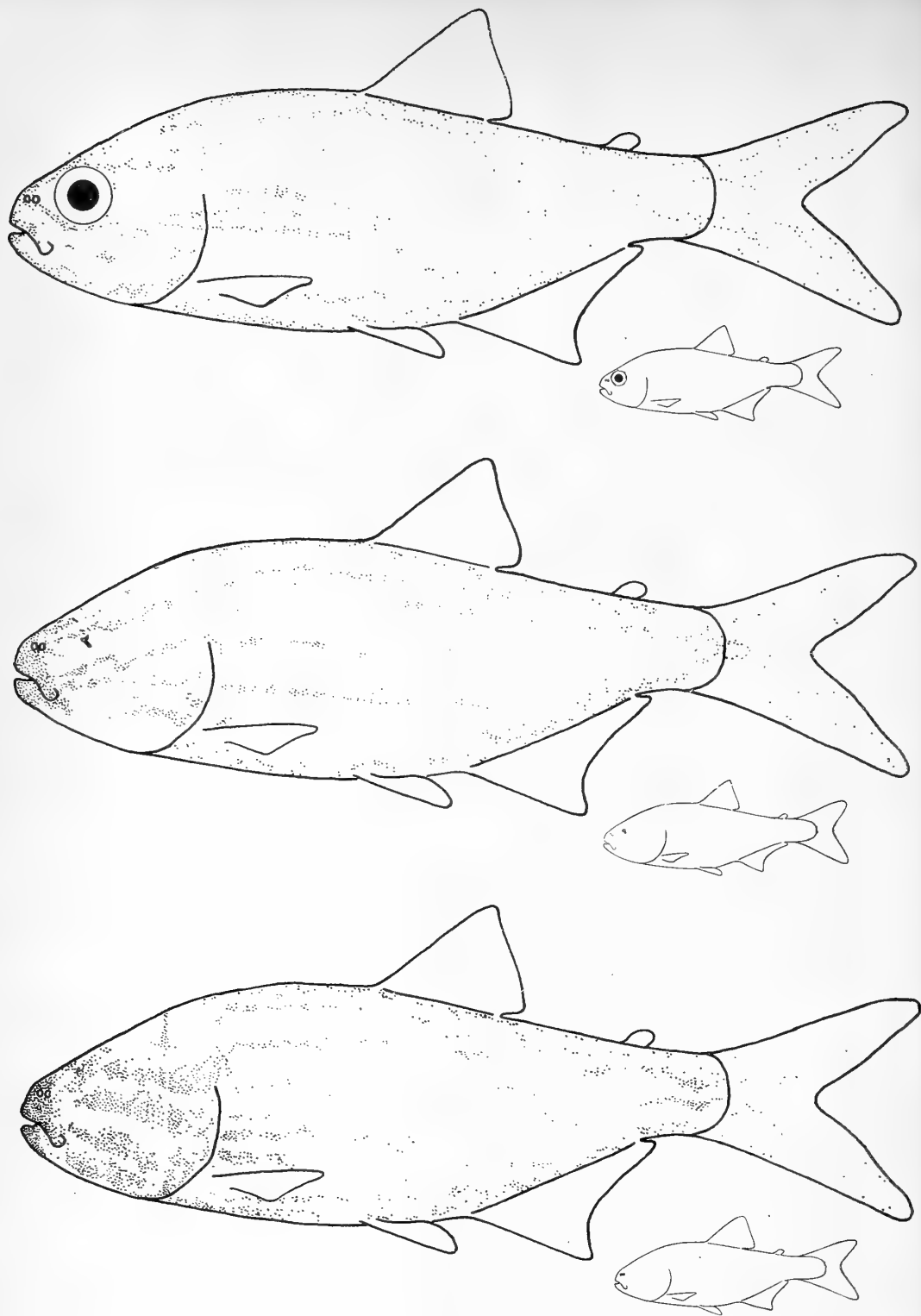
reinforced by the examination of other specimens in less detail.

The taste buds within the oral cavity, not figured, showed no significant change. In all three specimens and others the taste buds themselves showed no evident morphological change from one fish to another. There is, however, a marked change in the form of the taste buds of each fish, identical in nature, from one region of the body to another. These changes of form are indicated in Plate III. Those within the mouth are raised on little papilla-like mounds in the corium. Those embedded in the relatively thick epidermal covering of the head are merely pushed up to the general surface with which they are flush. Those on the body in the thin epidermal covering of the scales are broadened and flattened out in a manner suggestive of the neuromasts of the lateral-line canal but are much larger and histologically more clearly defined. So far as can be determined at this time these modifications of the exterior taste buds are merely an expression of mechanical responses to the thickness or other features of the epidermal layers in which they happen to be imbedded, excepting possibly those within the oral cavity which appear to be more highly developed.

### COMPARATIVE BEHAVIOR.

In order to attempt an evaluation of the significance of the chemical sensory apparatus of these fishes a series of experiments was undertaken on the reactions of the three types to various chemical stimuli. For this purpose normal fish from Cueva de los Sabinos and La Cueva Chica stock were employed as well as blinded river fish and anosmic La Cueva Chica specimens. Incidental to this it was found that river fish, in which the optic nerve had been severed, on recovery took on the essential wandering behavior of the naturally blind fish. That is, they commenced an incessant wandering very like that characteristic of the blind fish as reported by Breder and Gresser (1941a) and Breder (1943). The former, in studying light reactions, did not blind their river fish, with the result that they could not treat them in the same statistical manner as the cave fish. It would have been of no significance to their purposes, for when blinded, these fish become entirely indifferent to light as may be shown in a gradient trough. On the contrary, in present connections it is obvious that both experimental and control animals must operate without visual cues. These blinded river fish quickly became accommodated to their new status and lived on as well as the cave fish and found their food in an identical manner.

The anosmic fish were produced by means of electro-cautery of the nasal capsules. On recovery these showed little basic differ-



TEXT-FIG. 2. Distribution of exterior taste buds on Mexican characins. Upper: from Rio Tampaon, 34 mm. in standard length. Middle: from La Cueva Chica, 29 mm. in standard length. Lower: from Cueva de los Sabinos, 32 mm. in standard length. Reconstructed from serial sections. The small inserts represent the true outline of the fish in each case. The large outlines of identical nature are based on a typical form to which the taste bud distribution has been referred in order to facilitate comparison. See text for full explanation.

ence from the normal fish except that they did not find their food as quickly.

Beigel-Klaften (1913) discussed the regeneration of the nasal organ in *Tinca vulgaris* and in *Cyprinus carpio* Linnaeus. With the electro-cautery method employed in the present experiments, examination as well as the subsequent behavior which remained the same after several months showed there was clearly no reconstruction of the apparatus or ability to smell.

Much of the work on comparative behavior was undertaken in a trough 22 inches wide by 39 inches long with water to a depth of two inches. This was optically divided into two like compartments by means of a string drawn taut above the surface of the water so that there were, in effect, two parts, each 18½ inches by 22 inches. Burettes were suspended, one over the end of each, five inches from the end of the trough along its mid-line, so that the two sources of chemicals were 29 inches apart. In these troughs the positions of the fishes, in reference to the two compartments, were checked at five second intervals in a manner similar to that used by Breder and Gresser (1941a and b) for their studies on light reactions. In most of the experiments four fish were used at a time as more than that number were generally too difficult to keep accurate check on simultaneously. The end at which the chemicals were administered was alternated with each experiment in order to overcome any possible inherent bias in the trough.

For studies involving the circling movements of normal and semi-anosmic fishes another trough of 39 inches by 17 inches was employed, but which was otherwise similar.

After each experiment, the trough was flushed and tempered water was substituted for the contaminated water of the last test. The temperature of the water was maintained between 21° and 25° C. throughout the experiments described.

#### *Chemical Repellents.*

In the early exploratory part of the experiments it was found that acetic acid operated well as a repellent for these fishes and as a consequence it was largely used in these studies. Citric acid was also used but was found to show no advantage. Ammonium carbonate was also employed. The simplest and most satisfactory method of application tried was to allow dilute solutions to drip from a burette at as nearly a uniform rate as possible at one end of the trough while plain water from the trough dripped at a similar rate at the opposite end. Any possible, but not readily detectable, mechanical disturbance due to the slow inflow was thus compensated. The basic data of these experiments are given in

Tables I, III and IV together with pertinent data on quantities administered and pH values reached.

Table I gives the chemical and related data as well as the positions of the fish in percentage at the repellent end of the trough. Every experiment is designated by a number and letter. Each number indicates the use of a different substance or quantity. The letters indicate separate experiments, of which, in most cases, there were four of one kind. Each period of observation, of which there are eight, indicated at the right of the table, represents 100 observations at 5-second intervals. These values indicate the number of fishes recorded, expressed in percentage. Thus in experiment "1a" under period "1," the value 40 means that during the 100 observations made, 160 fishes were counted out of a possible 400 (4 fishes moving at random under such conditions would show 200 in one compartment or 50% of the total possible). All periods for each experiment, or horizontal row of figures, represents a period of 58 minutes and 20 seconds of observation. The even-numbered periods are consecutive with the preceding odd-numbered periods while an interval approximating a half hour represents the spacing of the beginning of each odd-numbered period. The means of each experiment thus represent an actual observation time of nearly two hours (1 hour, 53 minutes, 20 seconds) with 3,200 observations at five-second intervals.

Table III, together with other data to be discussed later, gives continuations of five of the tests that were carried on for longer periods, the longest reaching 1,900 observations over a period of more than two and one-half hours (2 hours, 37 minutes, 30 seconds), the latter of which were spread over longer units of time as is indicated in the table.

Table IV gives details of periods "5" and "6" of Tables I and II in eight smaller units together with other data. The horizontal rows of figures in this table are all consecutive and represent 200 observations with the means representing 800 observations.

A digest of this data is given in Text-figure 3. Graph A shows the retreat of the fishes during the actual acid-dripping period, based on Table IV, and indicates clearly the similarity in behavior between the blinded river fish, the normal fish from La Cueva Chica and those from Cueva de los Sabinos. It also indicates the difference in behavior of the anosmic fish as compared with the normals and the difference between the reactions of the normals to ammonium carbonate as compared to acetic acid.

Graph B treats the data of Table I in a

TABLE I. EXPERIMENTS WITH REPELLENTS.

Each figure concerning the distribution of fish represents 100 observations, the primary means, 400 and the secondary means, 800, except as indicated.

Exp. No.	FISH USED AND NO.	SUBSTANCE AND % SOL.	C.C. USED	PERCENTAGE OF FISH IN SUBSTANCE COMPARTMENT															
				PH CHANGES											PERIODS OF OBSERVATION				POST DRIP
				SUB. END		PERIOD 6		PERIOD 8		PRE-DRIP		SUB. DRIP		1	2	3	4	5	
SUB.	END	SUB.	BLANK	SUB.	BLANK	SUB.	END	SUB.	END	SUB.	END								
1a	4 blinded river fish	Acetic acid—10%	86	64	7.2	3.8	5.8	4.8	4.8	40	49	59	47	39	6	22	55		
1b			78	100	7.4	4.0	7.0	5.0	6.0	55	44	48	54	23	5	0	0		
1c			75	86	7.2	4.6	6.8	5.0	5.0	45	52	50	43	42	13	4	2		
1d			89	60	7.2	4.4	6.0	4.4	4.4	57	57	57	58	17	22	42 <sup>1</sup>	43		
	Primary means		82	78	7.3	4.1	6.4	4.8	5.0	49	50	54	51	30	11	17	25		
	Secondary means									50		52		21		21			
2a	4 La Cueva Chica fish (normal)	Acetic acid—10%	73	78	7.2	5.3	6.8	5.3	6.1	70	43	48	46	44	14	2	2		
2b			78	76	7.2	5.6	7.2	5.4	5.6	57	62	65	66	52	9	11	6		
2c			76	54	7.2	4.0	7.2	5.0	6.8	32	26	24	34	15	10	3 <sup>1</sup>	7		
2d			78	100	7.2	4.2	6.8	4.8	4.8	58	59	60	51	45	7	51 <sup>2</sup>	51		
	Primary means		76	77	7.2	4.8	7.0	5.1	5.8	54	48	49	49	39	10	17	17		
	Secondary means									51		49		24		17			
3a	4 La Cueva Chica fish (anosmic)	Acetic acid—10%	70	89	7.2	5.0	5.2	5.0	4.6	—	—	—	47	52	35	10 <sup>1</sup>	56		
3b			70	91	7.4	4.6	7.4	5.4	5.8	37	30	20	50	41	19	17	19		
3c			53	69	7.4	3.8	7.4	4.0	5.6	50	53	50	52	37	34	38	36		
3d			62	75	7.4	4.2	7.4	—	—	61	46	52	50	44	28	25	30		
	Primary means		64	81	7.3	4.5	6.9	4.8	5.3	49	46	42	51	39	23	35	35		
	Secondary means									46		45		31		35			
4a	4 Cueva de los Sabinos fish (normal)	Acetic acid—10%	99	85	7.4	4.0	5.6	4.4	4.8	52	65	66	60	41	8	29	54		
4b			76	100	7.2	5.2	7.2	5.4	6.4	59	61	29	41	29	8	2	2		
4c			89	88	7.0	4.0	6.4	4.2	5.0	35	47	34	44	27	13	2	2		
4d			71	79	7.2	5.4	7.2	5.0	5.8	42	51	72	62	40	6	3	1		
	Primary means		84	88	7.2	4.6	6.4	4.8	5.5	49	56	50	51	34	9	9	15		
	Secondary means									51		51		22		12			
5a	4 La Cueva Chica fish (normal)	Ammonium carbonate 10%	100	90	7.2	8.0	7.4	7.4	7.4	54	50	58	52	54	44	54	57		
5b			91	100	7.2	8.6	8.6	8.6	8.6	49	54	46	52	59	44 <sup>3</sup>	—	—		
5c			80	88	7.2	8.6	7.4	8.4	8.4	46	52	56	58	69	52	44	35		
5d			91	87	7.4	8.2	7.6	8.4	8.4	53	50	50	48	38	34	46 <sup>1</sup>	30		
	Primary means		90	81	7.3	8.3	7.7	8.2	8.2	51	51	52	55	44	48	41			
	Secondary means									51		52	49		44				
6	5 goldfish (normal)	Ammonium carbonate	50	—	7.0	7.4	7.2	7.4	7.4	—	—	50	48	56	76	36	32		
	Secondary means																		

1 Fish showed distress.  
2 Fish showed distress, with some mucus coagulation.  
3 Fish showed distress, one fish died and experiment was discontinued.  
4 Fish showed distress, three fish died, just at end of experiment.

TABLE II. EXPERIMENTS WITH ATTRACTANTS.

Each figure concerning the distribution of fish represents 100 observations, the primary means, 400 and the secondary means, 800, except as indicated.

EXP. NO.	FISH USED AND NO.	SUBSTANCE AND % SOL.	CC. USED	PH AT START AND END <sup>2</sup>	PERCENTAGE OF FISH IN SUBSTANCE COMPARTMENT								
					PERIODS OF OBSERVATION								
					PRE-DRIP			SUB. DRIP.		POST-DRIP			
			SUB.	BLANK		1	2	3	4	5	6	7	8
7a	4 blinded river fish	Cane sugar—40%	100	86	7.0	51	53	55	52	53	45	53	62
7b			100	96	7.0	52	46	52	48	60	51	64	62
7c			100	96	7.2	45	45	49	51	51	43	47	34
7d			120	93	7.2	49	53	50	50	55	53	44	51
	Primary means		105	93	7.1	50	49	52	50	55	48	52	52
	Secondary means					49		51		51		52	
8a	4 La Cueva Chica fish (normal)	Cane sugar—20%	70	71	6.8	—	—	51	45	53	50	56	53
8b			90	93	7.0	52	54	46	53	53	52	54	53
8c			93	87	7.0	50	52	54	55	62	53	48	45
8d			100	90	7.0	54	52	52	54	58	56	56	59
	Primary means		88	85	6.9	52	53	51	52	56	53	54	52
	Secondary means					52		51		54		53	
9a	4 La Cueva Chica fish (normal)	Cane sugar—40%	84	99	7.0	60	51	58	69	76	76	73	78
9b			70	56	7.0	50	48	52	52	54	52	53	55
9c			96	62	6.8	47	43	43	45	48	49	42	43
9d			92	68	7.0	50	48	53	55	53	58	54	57
	Primary means		85	71	6.9	52	47	51	55	58	59	55	58
	Secondary means					50		53		58		57	
10a	2 La Cueva Chica fish (anosmic) <sup>1</sup>	Cane sugar—40%	100	96	7.2	51	51	51	49	51	55	53	51
10b			93	69	7.2	50	51	49	49	50	53	56	52
10c			98	79	7.1	50	52	48	49	55	52	61	58
10d			100	86	6.8	50	53	50	57	57	50	53	62
	Primary means		98	82	7.1	50	52	49	52	53	53	56	56
	Secondary means					51		50		53		56	
11a	4 Cueva de los Sabinos fish (normal)	Cane sugar—40%	100	76	7.2	28	45	56	51	65	67	61	53
11b			100	100	7.2	47	37	45	41	40	49	55	49
11c			85	66	7.2	50	49	51	54	60	62	54	50
11d			100	100	7.4	46	49	35	34	35	39	29	31
	Primary means		96	85	7.3	43	45	47	45	50	54	50	46
	Secondary means					44		46		52		48	

<sup>1</sup> Each part of this experiment represents the mean of two experiments, combined here for purposes of this table, as to be comparable with the other experiments.

<sup>2</sup> Cane sugar would not change the pH values but they were checked at the end of each experiment for possible variations due to unknown causes. In all cases the pH values did not vary.

similar manner and serves to indicate the extent of the normal departure from the expected 50 percent. distribution that is found in these fishes by means of the four pre-drip or control periods in each case.

Graph C compresses the data of graph B to double periods and to that extent acts as a smoothing method. In other words, in this graph all the consecutive observations are treated as a unit. This serves to give a more general representation and reduces the incidental details more fully expressed in graph B.

Text-figure 5 show graphically the longer term experiments, the data of which are given in Table III.

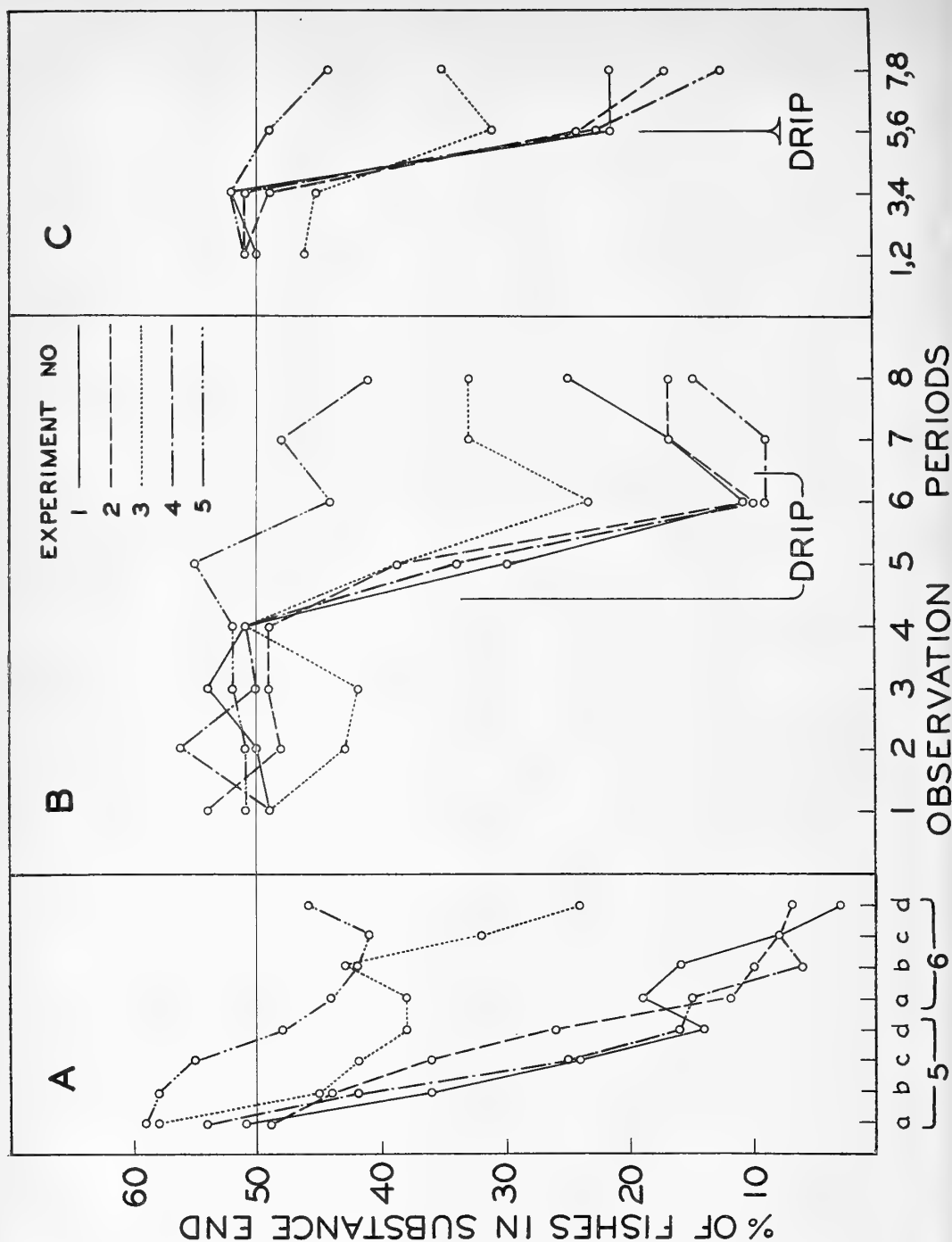
It is evident from Tables I and III that some of these experiments ran to the point of lethality. These effects are indicated in

foot notes to the tables. The word "distress" indicates that the fish began moving at higher than normal speeds with their snouts out of water and gave every evidence of being in serious difficulty. In certain cases the mucus became whitish as though coagulated and fell away in small pieces. In all, four fish died either during or immediately after experiments, as is indicated. All the rest survived and at this writing are still living. They gave evidence of rapid and complete recovery in all but the four cases noted.

The significance of these graphs is treated in the discussion.

#### Chemical Attractants.

Experiments with attractants were handled exactly as were those of the chemical repellents. The basic data of these are given



TEXT-FIG. 3. Reactions to chemical repellents. Graphic representation of the data of experiments 1 to 5 inclusive, based on Tables I and IV. Exp. 1—Blind river fish, 10% acetic acid. Exp. 2—La Cueva Chica fish, normal, 10% acetic acid. Exp. 3—La Cueva Chica fish, anosmic, 10% acetic acid. Exp. 4—Cueva de los Sabinos fish, 10% acetic acid. Exp. 5—La Cueva Chica fish, normal, 10% ammonium carbonate. Graph A: distribution of fishes during periods of the dripping administration of substances. Each point represents 100 observations. Graph B: distribution of fishes before, during and after the dripping administration of substances. Each point represents 400 observations. Graph C: distribution of fishes as in graph B but with all consecutive observations represented as a single point. Each point represents 800 observations.

in Tables II, III and IV, and the remarks under the previous head apply equally here. Dissolved prepared dry fish food, the juice of horse meat and cane sugar were used in these experiments. As no statistical difference was suggested in the early work, cane sugar was used for most of the experiments because of ease in standardizing.

A digest of these data is given in Text-figure 4 and is handled in a manner exactly comparable to that of the repellent agents. Text-figure 5 shows graphically the data of Table III.

Table V gives data on the circling movements of normal, anosmic and unilaterally anosmic fishes from La Cueva Chica stock. These experiments were performed in a simple trough. The stimuli, prepared dried food and cane sugar, was given in the solid form by allowing a small quantity to pass down a large glass tube with its end held near the floor of the trough at a time when the fish was at the far end of the trough. In each case a single fish was employed at a time. This was done because it was evident that the excited movements of a feeding fish served to attract the attention of others. This may be a lateral-line effect or could be due to the sound of chewing. The chewing sounds of the pharyngeal teeth of larger species may be heard quite distinctly through a simple "submarine listening tube" made of a stethoscope over the mouth of which is placed an ordinary unperforated nursing nipple.

The essential similarity in the behavior between the normal fish and the fully anosmic in respect to right and left hand turns as compared with the semi-anosmic is indicated in Text-figure 6. In conducting these experiments two fish were found, one in the normal group and one of the fully anosmic group, which showed a strong bias to circle to one side. Evidently there was some asymmetrical influence operating in the sensory mechanism of these individuals. For this reason they were omitted from the main body of the data and are so indicated in Table V and Text-figure 6.

The significance of these data is treated in the discussion.

#### CALCULATION OF RESULTS.

The numerical data obtained in the behavior experiments are capable of being analyzed in a number of respects additional to the simple estimation of the quantitative nature of the repellent or attractive stimulation of the chemical quantities employed.

Considering only the control periods which preceded the experiments, it is desirable to examine them in order to determine if, in spite of experimental precautions, any bias existed in the trough or in the behavior of the fish that might have a bearing on the results of the experiments.

Since it is expected that if there were no bias the fishes should be moving at random, and since in each case here considered there were four specimens in an optically divided trough of two like compartments, it follows that the numerical values of the observations should approximate 50 percent. The actual values observed for each of the four types of fishes used are given in Table VI. None shows any statistically significant departure and the mean of all was found to be 49.88+, that is, the fish were at one end of the tank as often as they were at the other.

Another measure of the presence of a possible bias is to consider the frequency of occurrence of the possible aggregation numbers as compared with the calculated values of the binomial distribution of four items. Since in any observation at one end there can be any of five possible numbers of fish, 0, 1, 2, 3 or 4, it follows from the equation for the binomial formula  $(p+q)^n$ , expanded for each term, that the observed occurrence of 0, 1, 2, 3 and 4 fish together at one end at one time should be 1, 4, 6, 4 and 1 or one chance out of 16 that there will be none, 4 out of 16 that there will be one and so on. The observed values are given in Table VI, from which it is clearly evident that they closely approach the calculated expectancy: 6.25, 25, 37.5, 25, 6.25, being 7, 25, 36, 25, 7. Since the experiments were all carried out using first one and then the other end of the trough, any bias in it would appear if the values obtained at one end be compared with those of the other. Designating one end as "A" and the other as "B," this comparison is also made in Table VI. That there is no significant difference from one end to the other is evident. In this same table there is also given a comparison of all the observations for each form studied. These calculations are shown graphically in Text-figure 7, both with regard to each form of fish and with regard to the trough end. The slight divergencies are clearly indicated. Only in those experiments involving small numbers of observations are any notable divergencies from the binomial values to be seen. Such as are present have a distinct bearing on the problem, but only become clear in the following further analysis.

It was evident during these control periods that each type of fish did not act exactly as every other in respect to their attitudes to their fellows. The above calculations give scant indication of this, however, since whether the fish were acting strictly independently or with some slight degree of unanimity could hardly be expected to show clearly in such a treatment. If the fish were fully tied together, optically or by other means, such behavior would, of course, be evident at once from these fig-

TABLE III. LONG TERM EXPERIMENTS.

Period numbers continue from Tables I and II. This is a continuation of the experiments indicated of those tables and the notation is exactly the same.

EXPERIMENT NUMBER	9	10	11	12	13	14	15	16	17	18	19	20
La Cueva Chica												
2a (acid)	3 <sup>1</sup>	2	24	22	35	25	20	30	24	26	11	22
2b	30	36	51 <sup>1</sup>	65	51	46	40	44	39	43	51	53
2c	2	0	19 <sup>1</sup>	8	39	34	40	45	52	41	55	62
Pri. means	12	13	31	32	42	35	33	40	38	37	39	46
Sec. means	12		32		39		37		38		42	
La Cueva Chica												
8a (sugar)	51	56	36	44	51	55	41	40	47	40		
Sec. means	54		40		53		40		44			
River Fish												
1a (acid)	44	44	45 <sup>2</sup>	50	54	68						
Sec. means	44		49		61							

DIFFERENCE IN MINUTES BETWEEN START OF READINGS.

Even numbered readings continuous with preceding odd numbered periods. Odd numbered periods in Tables I and II started about 30 minutes apart, with the following even numbered periods continuous with them.

EXPERIMENT NUMBER	1	3	5	7	9	11	13	15	17	19
2a	—	25	40	25	40	65	55	60	60	60
2b	—	30	40	30	30	75	45	60	60	60
2c	—	25	40	30	30	70	50	60	60	60
Means		27	40	28	33	70	50	60	60	60
8a	—	45	30	30	70	50	60	60	60	
1a	—	25	40	30	30	65	55			

<sup>1</sup> Fish showed distress.

<sup>2</sup> Fish showed distress, with some mucus coagulation.

ures, for instead of a binomial distribution of four items one should obtain a distribution of one item. In other words the figures would indicate the behavior of a school, of four fishes in this case, which under the conditions would give a 1 to 1 distribution value. If the linkage were not as perfect as this case, which might be expected to obtain in a school of herring or mackerel, the values should approach one of the intermediate binomial distributions. Thus with four fish it could be possible to have any of the following frequencies depending on the cohesiveness of the group: 1-1; 1-2-1; 1-3-3-1; 1-4-6-4-1 displaced on the scale of 0 to 4 appropriately. That there is no evidence of a tendency toward the first three possibilities is apparent. The following tabulation of these possibilities and their significance should make this entirely clear.

POSSIBLE FREQUENCIES	SIGNIFICANCE
1-1 1 aggregation.	Four fish stay close together.
1-2-1 2 aggregations.	Groups of 2 and 2 or 3 and 1.
1-3-3-1 3 aggregations.	Groups of 2, 1 and 1.
1-4-6-4-1 4 aggregations.	Four "groups" of 1 fish each.

Attacking the problem in another way, it became apparent in the original pages of

data that in certain cases consecutive observations showed the same number of fishes together for more or less extended time. These sequences of consecutive observations of certain numbers of fish indicated that when the fishes came close together they tended to remain there, which gives some measure of a slight and otherwise scarcely detectable aggregating tendency. This tendency appeared to differ in the various forms. Although this part of the analysis was undertaken because of what appeared to be behavior differences noted during the carrying out of the experiments, the statistical analysis led to a different interpretation of the condition than that based on simple observations.

The mathematical analysis of the occurrence of these sequences of observations of the same number of fish is slightly more complicated than the preceding study of the distribution of the aggregations but is a further rendering of the binomial equation. Since the likelihood of a given event recurring in sequence in such a study is  $p^n$ , it is possible to compare the observed sequences in regard to both their duration in time and number of times they appear in the observations to the probability values obtained for each of the five possible num-



TABLE IV. SHORT TERM PERIODS DURING THE ADMINISTRATION OF SUBSTANCES

Each of these periods are one-quarter the length of those of Tables I and II. They are indicated as lettered parts of periods 5 and 6 of those tables. Each figure represents 25 observations, the means 100.

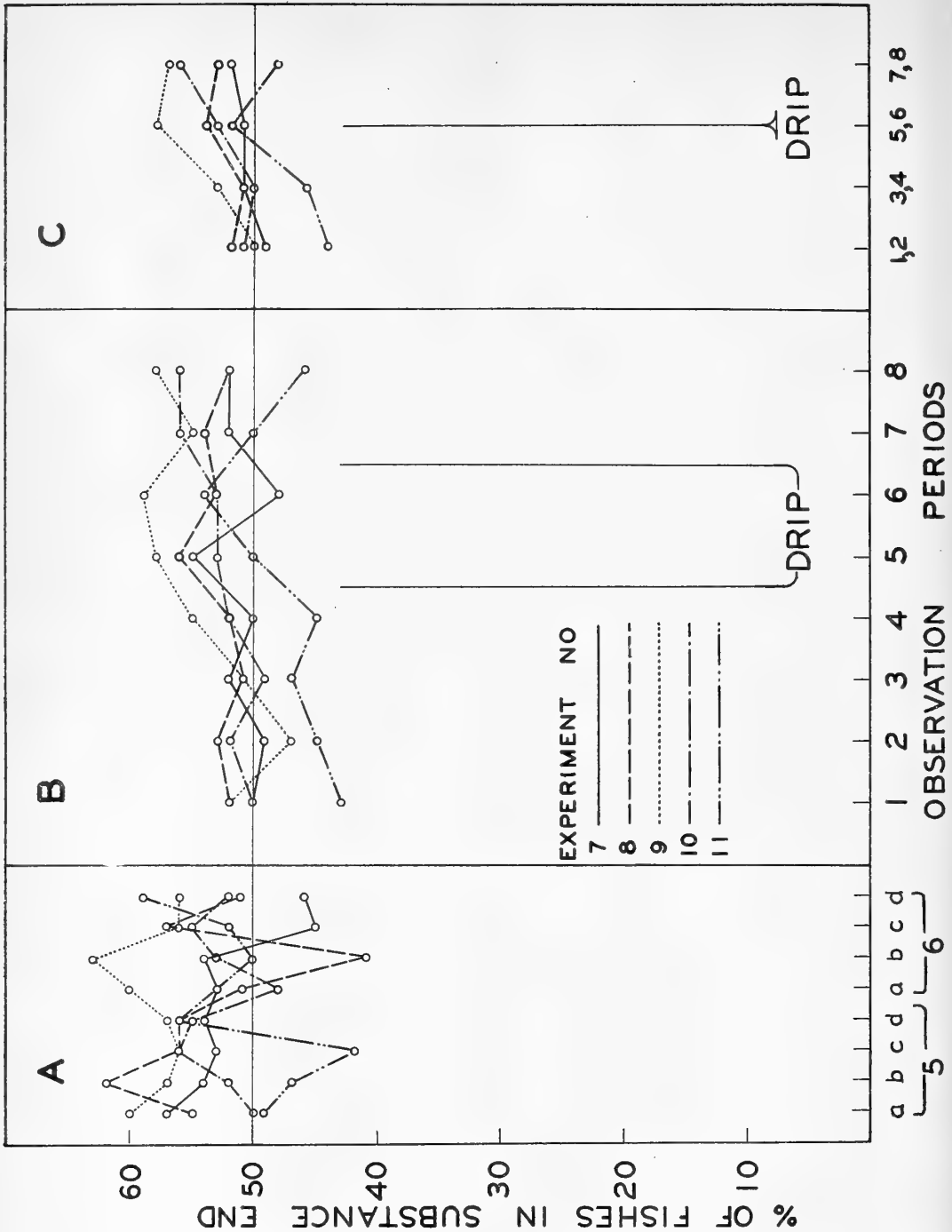
EXP.	DRIP PERIODS								EXP.	DRIP PERIODS							
No.	5a	5b	5c	5d	6a	6b	6c	6d	No.	5a	5b	5c	5d	6a	6b	6c	6d
1a	56	57	27	17	13	6	3	2	7a	50	56	52	54	56	40	34	48
1b	46	16	19	10	13	3	2	2	7b	68	54	50	67	56	54	44	52
1c	52	50	43	25	11	15	18	7	7c	60	46	52	47	45	49	52	27
1d	47	21	8	3	40	37	11	0	7d	52	59	57	50	55	52	49	56
Means	51	36	24	14	19	16	8	3		57	54	53	54	53	54	45	46
2a	56	37	49	31	17	18	15	7	8a	56	56	54	59	44	49	64	54
2b	48	60	63	39	19	9	5	5	8b	52	61	50	48	54	41	58	54
2c	33	13	2	12	9	11	9	9	8c	59	69	61	59	55	56	54	46
2d	60	64	31	23	4	10	5	9	8d	53	62	58	59	52	49	53	71
Means	49	44	36	26	12	10	8	7		55	62	56	56	51	41	57	51
3a	54	47	70	75	65	73	49	38	9a	75	66	85	77	77	81	80	67
3b	75	42	31	17	19	30	17	8	9b	56	57	46	57	57	57	44	49
3c	50	40	24	35	26	40	37	35	9c	50	51	42	47	46	56	45	50
3d	53	50	45	26	31	31	24	24	9d	58	56	47	59	59	59	56	59
Means	58	45	42	38	38	43	32	42		60	57	56	57	60	63	56	56
4a	54	50	33	27	15	3	6	9	10a	42	53	54	56	56	54	52	58
4b	53	40	16	8	17	5	8	6	10b	43	58	49	51	33	59	56	66
4c	34	32	26	16	16	11	13	11	10c	56	50	62	55	56	55	52	43
4d	76	49	24	12	12	4	4	4	10d	58	49	60	60	48	44	61	50
Means	54	42	25	16	15	6	8	7		50	52	56	55	48	53	55	52
5a	55	64	48	49	42	39	41	52	11a	66	69	60	64	66	63	63	77
5b	62	60	60	53	41	47	41	48	11b	48	28	38	46	34	43	53	64
5c	80	74	68	56	68	55	35	52	11c	50	57	57	75	66	65	64	55
5d	38	36	44	33	27	27	48	33	11d	33	33	35	38	48	30	37	41
Means	59	58	55	48	44	42	41	46		49	47	42	56	53	50	52	59

bers of fish in a group occurring  $n$  times in succession. Divergencies from the calculated values of significant magnitude then appear in two ways: (1) as numbers of times that a sequence of any given length occurs above expectation and (2) actual length of the longer sequences compared with the probability of such a length of sequence occurring at all. The data so obtained for the various experiments of each possible observation in regard to the occurrence of sequences of various lengths is given in Table VII. In this table each experiment is indicated together with the number of times of occurrence of each sequence for every length of sequence observed. In Experiment 1, for example, no fish were at one end of the trough for one observation only 52 times, for a sequence of two observations 17 times and so on, while all four fish were together for one observation only 54 times and for two observations 24 times. Since, obviously, for each set of readings, given in this table, there is another, at the opposite end of the trough, which represents the difference between the total number of fishes, four, minus those indicated in Table VII, it is possible to combine these values and reduce the data to the form given in Table VIII in which

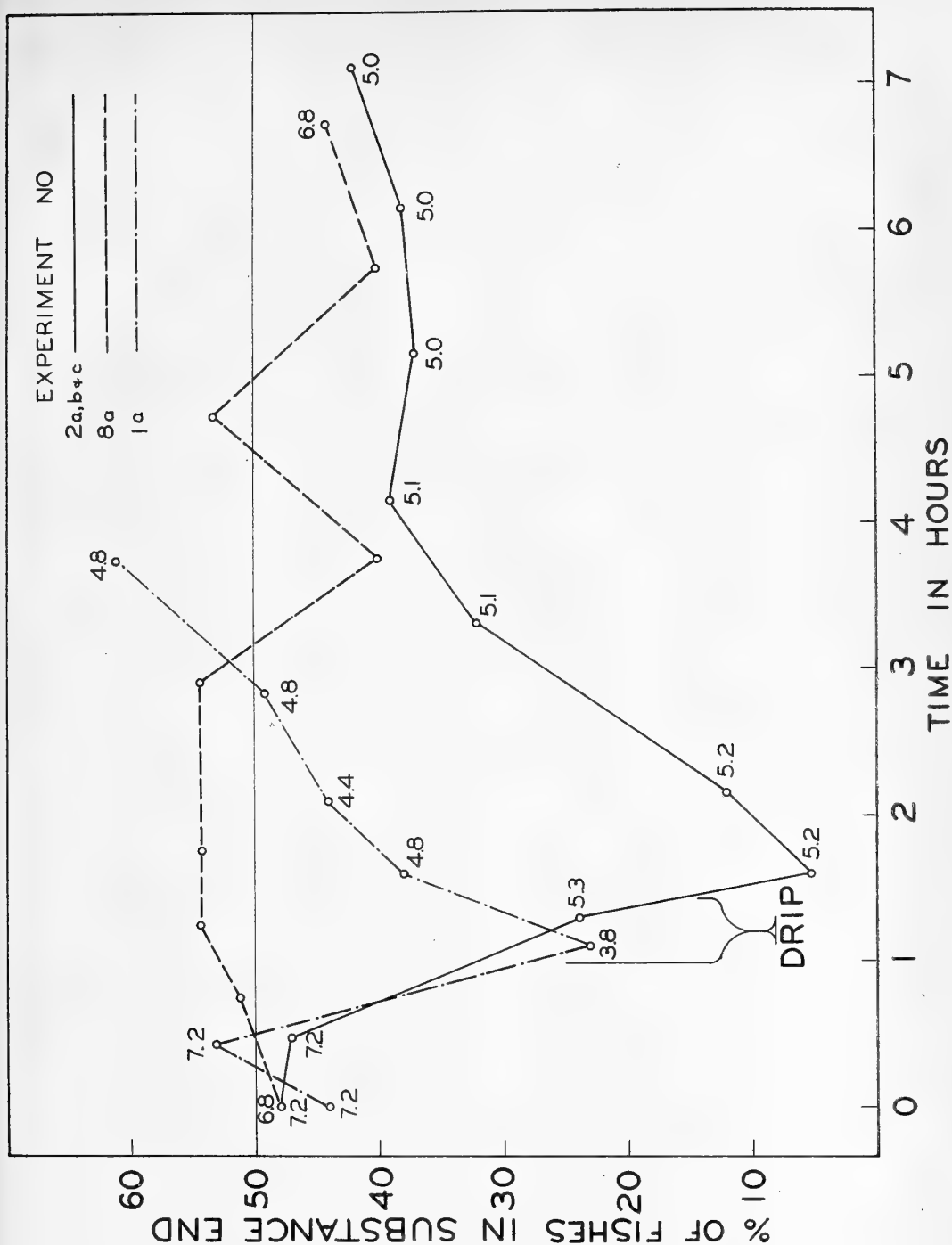
only three sets of figures for each experiment need be handled.

Reducing the calculated probability values to terms in which the first power is equated to unity for each of the different kinds of combinations possible (2 fishes, the mean of 1 and 3 fishes and the mean of 0 and 4 fishes), it is possible to compare these calculated values directly with the observed values by equating the number of single observations (sequences of one) to unity. These figures, based on both observed and calculated values, are given in Table IX, in which the calculated values for each class of data are directly comparable to the observed values for that class. The evident differences show the increase of the observed values both in number of sequences and their length beyond expectancy.

It is evident that while the river and Cueva de los Sabinos fish are closely similar and differ only slightly from binomial expectancy, La Cueva Chica material shows a greater divergence and the anosmics show extreme variance. If the calculated values are subtracted from the observed, then these differences, if positive, show the extent of the observed over the expected and, if negative, the reverse. These values are given in Table X and graphically shown in



TEXT-FIG. 4. Reactions to chemical attractants. Graphic representation of the data of experiments 7 to 11 inclusive, based on Tables II and IV. Exp. 7—Blind river fish, 40% sugar. Exp. 8—La Cueva Chica fish, normal, 20% sugar. Exp. 9—La Cueva Chica fish, normal, 40% sugar. Exp. 10—La Cueva Chica fish, anosmic, 40% sugar. Exp. 11—Cueva de los Sabinos fish, 40% sugar. Graph A: distribution of fishes during periods of the dripping administration of substances. Each point represents 100 observations. Graph B: distribution of fishes before, during and after the dripping administration of substances. Each vertical division four times the size of those in graph A. Each point represents 400 observations. Graph C: distribution of fishes as in graph B but with all consecutive observations represented as a single point. Each point represents 800 observations.



TEXT-FIG. 5. Long term experiments with repellents and attractants. Graphic representation of the data of experiments 1a, 2a, b and c and 8a, based on Tables I, II and III. Exp. 2a, b and c—La Cueva Chica fish, normal, acetic acid 10%. Exp. 8a—La Cueva Chica fish, normal, sugar 20%. Exp. 1a—Blind river fish, acetic acid 10%. Each point of experiments 1 and 8 represents 200 observations and of 2 each point represents 600 observations. The verticals which have been referred to a time scale are equivalent to those used in graph C of text-figures 3 and 4. The figures at each point indicate the pH value at that time at the end of the trough remote from the administration of the substance.

TABLE V. INFLUENCE OF NOSTRILS ON SWIMMING DIRECTIONS.

Each sub-experiment covers an interval of five minutes. Clockwise turns in the case of the left anosmic are with the intact nostril to the inside of the turn. The normals and left anosmics found food in the first interval and were then discontinued. The full anosmics did not find food through three sub-experiments. In no case was the sugar actually found because of its going into solution. For this reason the full anosmics were omitted from this test.

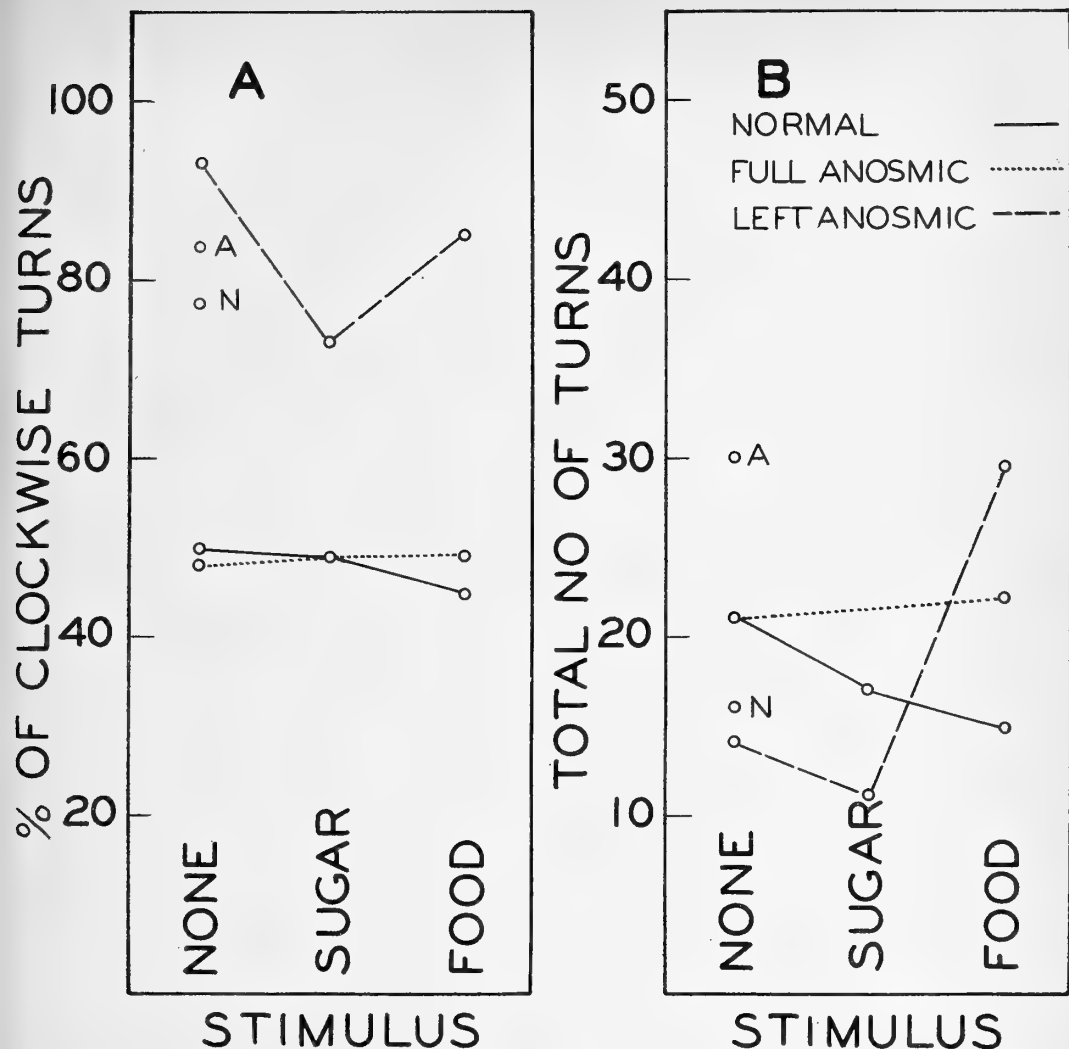
EXP. NO.	FISH	STIMULUS	TURNS CLOCKWISE	TOTAL TURNS	PER CENT CLOCKWISE
12a	Normal	None	9	18.5	48.6
12b			12	23.5	51.1
		Means		21	50
13a	Left anosmic	None	15	15	100
13b			10.5	13.5	85.2
		Means		14	93
14a	Full anosmic	None	10.5	21.5	53.5
14b			9	21.5	41.8
		Means		21	48
15a	Normal	Cane sugar	8	16	50
15b			10	19.5	51.3
15c			6.5	14.5	44.8
		Means		17	49
16a	Left anosmic	Cane sugar	6	10.5	57.2
16b			11.5	12.5	92
16c			8	11.5	69.6
		Means		11	73
17	Normal	Food	6.5	14.5	44.8
18	Left anosmic	Food	25	29.5	84.9
19a	Full anosmic	Food	7.5	20	37.5
19b			14.5	24	60.4
19c			10.5	21.5	48.8
		Means		22	49
20a	Biased normal	None	11	17	64.6
20b			14.5	17.5	82.8
20c			11	13	84.6
		Means		16	77
21	Biased full anosmic	None	25	30	83.4

Text-figure 8. Here in effect the calculated values are represented by the horizontal "O." A full discourse on these implications is reserved for the discussion, but the following may be noted here. This type of analysis clearly shows that all exceeded the calculated values but that while the river and Cueva de los Sabinos fish showed the least departure from expectancy, the anosmics showed the most and were approached by La Cueva Chica normals. Observations at the time of the experiments seemed to indicate that the first two actually gave more heed to their fellows than did the others. This gave an appearance of an aggregating tendency but this analysis, on the other hand, could be taken to indicate that the anosmics grouped more than the others. Evidently what appeared to the eye in observing the fishes was that the river and Cueva de los Sabinos fish detected each other with greater certainty or at a greater distance from each other but, nevertheless acted with greater individual independence.

Thus what was actually seen was evidently these fishes turning toward each other or attempting to avoid collisions. This feature has considerable bearing on certain of the aspects of the effects of repellents and attractants which is subsequently developed.

This method of analysis is not useful for the periods involving application of substances or in the post-application periods because of the increasing complication arising from the presence of a gradient in time and space of the chemical involved to which can be assigned no accurate numerical value. In other words, since the fish were pushed or pulled toward one end of the trough, the significant separation of the effects of the chemicals from those of aggregating tendencies becomes impossible by this method. The simpler treatment of employing arithmetical means, furthermore, suffices for the later periods.

No significant correlations could be established between the various experiments or their parts that bore any relationship to



TEXT-FIG. 6. Circling movements of normal, anosmic and unilaterally anosmic fishes and their relative number per unit of time. Graph A: percent of turns toward the intact nostril of semi-anosmics as compared with similar turns of normal and fully anosmic fish in reference to various stimuli. Graph B: total number of turns per five minute interval of the three types of fish in reference to various stimuli. Based on the data of Table V. See text for full explanation.

the slight variations in the pH values reached or the number of cc. used as recorded in Tables I and II. Evidently these differences were all below any value that might be expected to show measurable differences in the fishes' behavior by the methods here employed.

An analysis of the frequency distributions of the data of Tables I and II and the original figures on which they are based showed no significant differences in dispersion coefficients. Consequently calculations of the standard deviations are omitted.

## DISCUSSION.

It is notable that the extent of reactions to repellents as compared with attractants is much more marked in the former, as may be seen by a comparison of Text-figures 3 and 4. This would be expected since a repellent would be operative under practically any circumstance while the extent of influence of such an attractant as might be used would depend on many factors, considering what slight influences will stop feeding reactions in fishes. Such items as extent of hunger, fright, sexual or other conditions

TABLE VI. DISTRIBUTION OF FISHES DURING CONTROL PERIODS.

		ARITHMETIC MEANS									
Blinded river fish (Exp. 1 & 7; periods 1 to 4).....		50.50									
La Cueva Chica normals (Exp. 2, 5, 8 & 9; periods 1 to 4).....		51.08+									
La Cueva Chica anosmics (Exp. 3 & 10; periods 1 to 4).....		48.07—									
Cueva de los Sabinos (Exp. 4 & 11; periods 1 to 4).....		48.06+									
All (Exp. 1, 2, 3, 4, 5, 7, 8, 9, 10 & 11; periods 1 to 4).....		49.88+									

		DISTRIBUTION OF AGGREGATIONS									
EXP. NO.	NO. OF OBS.	AGGREGATIONS OBSERVED					AGGREGATIONS IN PERCENT				
		0	1	2	3	4	0	1	2	3	4
1	1600	101	386	589	412	112	—	6	24	37	26
2	1600	156	389	496	418	141	—	10	24	31	26
3	1400	112	384	364	276	64	—	8	27	40	20
4	1600	121	396	510	432	141	—	7	25	32	27
5	1600	96	368	605	410	121	—	6	23	38	26
6	200	54	27	24	14	28	53	27	13	12	7
7	1600	85	407	617	387	104	—	5	25	39	24
8	1400	71	333	520	386	90	—	5	24	37	28
9	1584	88	359	619	393	125	—	5	23	39	25
10	3200	746	1667	787	—	—	—	23	52	25	—
11	1600	191	440	543	345	81	—	12	27	34	22

AGGREGATIONS GROUPED BY FORMS					
Blinded river fish (3200 observations)	6	25	37	25	7
La Cueva Chica normals (6184 observations)	7	23	36	26	8
La Cueva Chica anosmics (1400 observations)	8	27	40	20	5
Cueva de los Sabinos (3200 observations)	10	26	33	24	7
All (13984 observations)	7	25	36	25	7
Calculated expectancy	6.25	25	37.5	25	6.25

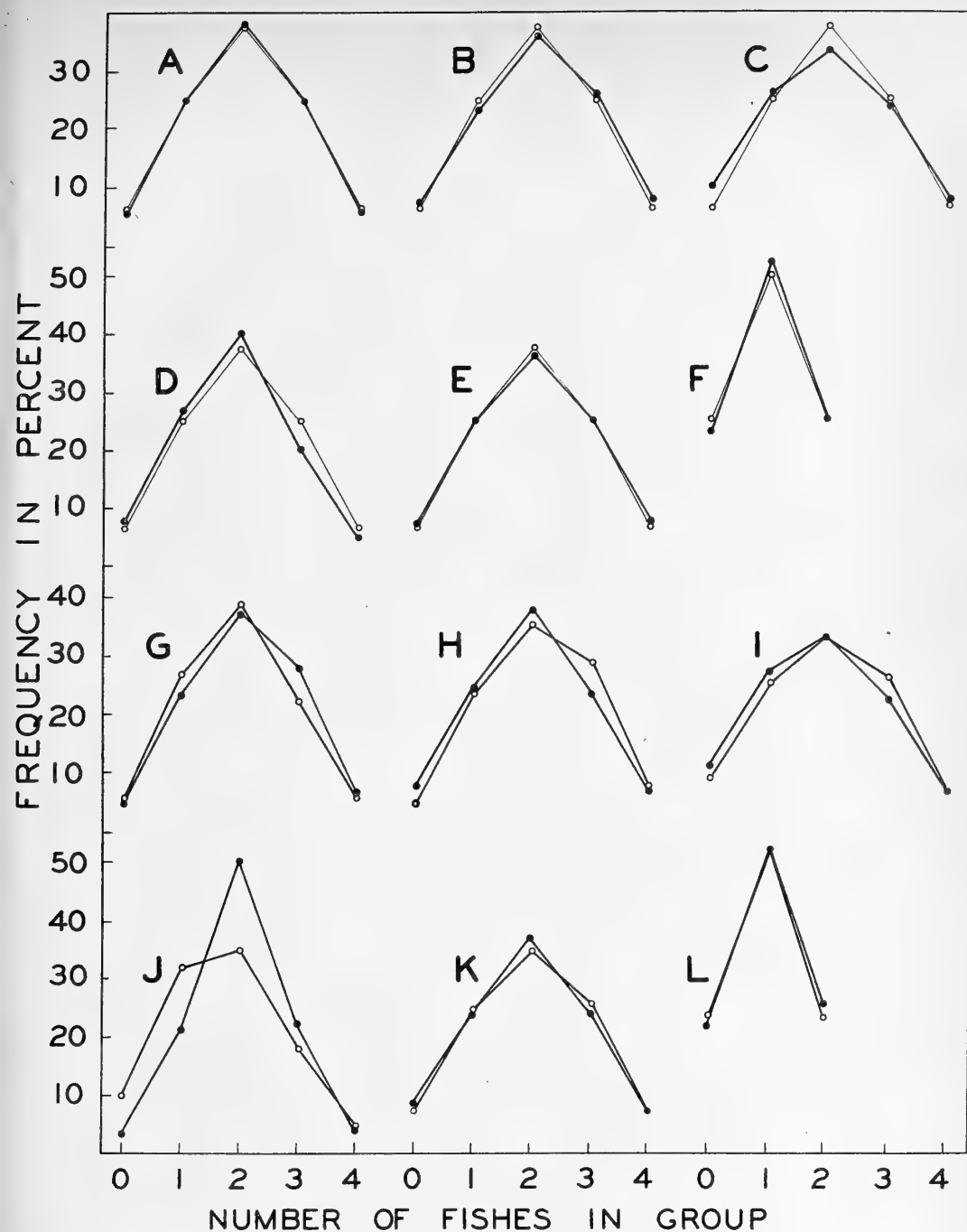
AGGREGATIONS GROUPED BY TROUGH END					
Blinded river fish ("A" end; 1600 obs.)	6	27	39	22	6
Blinded river fish ("B" end; 1600 obs.)	5	23	37	28	7
La Cueva Chica normals ("A" end; 3000 obs.)	5	23	35	29	8
La Cueva Chica normals ("B" end; 3184 obs.)	8	24	38	23	7
La Cueva Chica anosmics ("A" end; 800 obs.)	10	32	35	18	5
La Cueva Chica anosmics ("B" end; 600 obs.)	3	21	50	22	4
La Cueva Chica anosmics ("A" end; 1600 obs.)	24	52	24	—	—
La Cueva Chica anosmics ("B" end; 1600 obs.)	22	52	26	—	—
Cueva de los Sabinos ("A" end; 1600 obs.)	9	25	33	26	7
Cueva de los Sabinos ("B" end; 1600 obs.)	11	27	33	22	7

all would be expected to have more or less inhibitory effects from time to time. In other words a repelling influence would be expected to have a more consistently definite effect than a potentially equally attractive influence.

Since integumentary response in fishes is lodged both in the taste buds and in the nerve endings of the "common chemical sense," the latter of which is evidently only stimulated by sour, saline and alkaline solutions, Parker (1922), these skin sensations require some discussion. It was not feasible in our work to attempt experimentally to separate these two sensory systems, nor would it have served any important purpose in the present study. This condition may well represent, however, a further reason for the difference in the magnitude of the reactions to a sour and a sweet substance. In this connection it should be borne in mind that Strieck (1924 and 1925) has shown that *Phoxinus* can recognize sub-

stances ordinarily tasted, by means of the nasal organs alone, since in water any chemical is freely presented to both receptors because both are bathed in a common solution.

Considering first the retreat of these fishes before an increasing gradient of acetic acid, it is evident that there is no clear statistical difference between the normal fishes, in respect to nostrils and taste buds, of any of the three types under study. Three kinds of irritation may enter into this avoiding reaction; taste bud influences, nasal pit influences and general skin irritation, "the common chemical sense." The differences in taste bud number and the nature of the nasal pits, between the three types, would hardly be expected to show a graphic difference by this manner of treatment. However, it must be admitted, graphs B and C of Text-figure 3, which are based on the largest body of data and least subject to incidental influ-



TEXT-FIG. 7. Observed frequency distribution of fishes in all possible groupings compared with the calculated binomial distribution of the same number of items. Based on the data of Table VI. Graphs A to F: distribution of fishes by forms (dark circles and heavy lines) compared with binomial distribution (open circles and light lines). A: blinded river fish, experiments 1 and 7. 3,200 observations. B: La Cueva Chica fish, experiments 2, 5, 8 and 9. 6,184 observations. C: Cueva de los Sabinos fish, experiments 4 and 11. 3,200 observations. D: anosmic fish, experiment 3. 1,400 observations. E: all above experiments, 1, 2, 3, 4, 5, 7, 8, 9 and 11. 13,984 observations. F: anosmic fish, experiment 10. 3,200 observations. Graphs G to L: distribution of fishes by forms in reference to end of trough employed. Open circles represent the "A" end and dark circles the "B" end. G: blinded river fish, experiments 1 and 7. "A," 1,600 observations. "B," 1,600 observations. H: La Cueva Chica fish, experiments 2, 5, 8 and 9. "A," 3,000 observations. "B," 3,184 observations. I: Cueva de los Sabinos fish, experiments 4 and 11. "A," 1,600 observations. "B," 1,600 observations. J: anosmic fish, experiment 3. "A," 800 observations. "B," 600 observations. K: all above experiments, 1, 2, 3, 4, 5, 7, 8, 9 and 11. "A," 7,000 observations. "B," 6,984 observations. L: anosmic fish, experiment 10. "A," 1,600 observations. "B," 1,600 observations.









TABLE VII. OBSERVED DISTRIBUTION OF SEQUENCES.

EXP. NO.	No. OF FISH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	20	24	26	31
1	0	52	17	2	1	1														
	1	152	55	16	14	4														
	2	198	73	38	12	7	3	1	—			1	1							
	3	154	60	30	8	2	1													
2	4	54	24	2	1															
	0	13	15	11	6	3	1	2	—	1	—	—	1							
	1	66	44	22	11	2	5	3	3	1	2	1								
	2	99	49	35	15	11	4	3	2	2										
3	3	70	31	25	14	5	7	1	3	1	—	1	—	1	—	—	—	1		
	4	17	12	9	4	3	1	2	—	—	1	—	1							
	0	17	7	4	5	—	2	—	—	—	—	1	—	—	—	—	—		1	
	1	56	36	20	14	3	6	1	2	3	—	1	—	—	—	1				
4	2	101	48	21	13	13	6	3	4	1	2	1	—	1	—	—	—	—		
	3	58	32	11	10	6	2	2	2	1										
	4	15	13	2	1	1	—	—	1											
	0	38	20	6	2	1	2													
5	1	139	46	24	8	5	2	1	1	1										
	2	185	79	26	10	2	3	3												
	3	115	51	34	6	8	7	1												
	4	55	15	5	5	3	1													
6	0	36	19	3	2	1														
	1	121	51	23	8	4	4													
	2	142	85	44	22	7	1	1	2	1										
	3	125	56	28	6	6	1	3	1											
7	4	48	17	10	1	1														
	0	1	3	1	1	3	—	—	—				1	1						
	1	6	3	2	—	—	—	—	—	1										
	2	5	3	3	1															
8	3	5	2	—	—	1														
	4	3	2	2	1	1	1													
	5	—	2	—	1	1	1	—	—	—	—	—	—			1	—	1		
	0	47	16	2																
9	1	166	61	26	9	1														
	2	208	98	27	18	5	4			—		1								
	3	163	74	19	2	1	1													
	4	60	18	1	1															
10	0	48	6	1	2	—	1													
	1	153	53	12	8	—	1													
	2	213	65	32	12	4	1	1												
	3	164	68	29	5	—	1													
11	4	178	60	13	1	3		1	1											
	0	337	144	33	4	—	1													
	1	360	195	96	59	34	17	6	3	2	1	1	—	—	—	1				
	2	358	127	32	13	4	—	1												
12	0	88	23	11	3	1	—	1												
	1	179	61	21	10	2	2	2												
	2	204	75	26	11	9	1	1	—	1										
	3	161	51	17	5	1	1													
13	4	56	7	1	2															

TABLE VIII. COMBINED SEQUENCES OF OBSERVED DISTRIBUTIONS.

No. OF FISH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	24	26	31
Blinded river fish (Exp. 1 & 7)																		
2	406	171	65	30	12	7	1	—	—	—	2	1						
Mean 1 - 3	317.5	125	45.5	16.5	4	1												
Mean 0 - 4	106.5	37.5	3.5	1.5	0.5													
La Cueva Chica (Exp. 2, 5, 8 & 9)																		
2	665	293	145	61	29	7	8	5	3									
Mean 1 - 3	513	221.5	78.5	30	9	10.5	4	4	1	1	1	—	0.5	—	—	0.5		
Mean 0 - 4	168	56	21	8	5.5	1	2	—	0.5	0.5	—	1						
Anosmics (Exp. 3)																		
2	57	34	15.5	12	4.5	4	1.5	2	2	—	1	—	1	1	—	—	—	1
Mean 1 - 3	101	48	21	13	13	6	3	4	1	2	0.5	0.5	—	—	—	0.5		
Mean 0 - 4	16	10	33	0.5	—	—	0.5	—	—	—	—	—	—	—	—	—	0.5	
Anosmics (Exp. 10)																		
1	360	195	96	59	34	17	6	3	2	1	1	—	—	—	1			
Mean 0 - 2	347.5	135.5	37.5	8.5	—	—	0.6											
Cueva de los Sabinos (Exp. 4 & 11)																		
2	389	154	52	21	11	4	4	—	1									
Mean 1 - 3	297	104.5	48	14.5	8	6	2	0.5	0.5									
Mean 0 - 4	118.5	32.5	11.5	6	2.5	1.5	0.5											

TABLE IX. OBSERVED SEQUENCES AND CALCULATED BINOMIAL DISTRIBUTION.

CALCULATED BINOMIAL DISTRIBUTION (FIRST POWER = UNITY)

POWER	FOUR ITEMS			TWO ITEMS	
	2	1 - 3	0 - 4	1	0 - 2
1	1.00000	1.00000	1.00000	1.00000	1.00000
2	.37500	.25000	.06250	.50000	.25000
3	.14062	.06250	.00392	.25000	.06250
4	.05273	.01562	.00024	.12500	.01562
5	.01978	.00392	.00002	.06250	.00392
6	.00742	.00098	.00000	.03125	.00098
7	.00278	.00024		.01562	.00024
8	.00104	.00006		.00781	.00006
9	.00039	.00002		.00392	.00002
10	.00015	.00000		.00195	.00000
11	.00005			.00098	
12	.00000			.00048	
13				.00024	
14				.00012	
15				.00006	
16				.00003	
17				.00001	
18				.00000	

OBSERVED DISTRIBUTION OF FISHES. (NO. OF SINGLE OCCURRENCES = UNITY)

SEQUENCE OF FISHES	2	MEAN 1-3	MEAN 0-4	2	MEAN 1-3	MEAN 0-4	1	MEAN 0-2
	River	(1 & 7)		Chica	(2, 5, 8 & 9)		Anosmics (10)	
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2	.422	.394	.352	.442	.432	.333	.542	.389
3	.160	.143	.033	.218	.153	.120	.268	.093
4	.074	.052	.014	.096	.058	.048	.164	.024
5	.026	.013	.005	.044	.018	.033	.095	.006
6	.017	.003		.010	.020	.006	.047	.002
7	.002			.012	.008	.012	.017	.002
8	—			.008	.008	—	.008	
9	—			.005	.002	.003	.006	
10	—				.002	.003		
11	.005				.002	—		
12	.002				—	.006		
13					.001			
24					.001			
Sabinos (4 & 11)				Anosmics (3)				
1	1.000	1.000	1.000	1.000	1.000	1.000		
2	.385	.352	.274	.476	.685	.625		
3	.131	.160	.097	.208	.272	.187		
4	.054	.049	.051	.128	.211	.187		
5	.028	.027	.021	.128	.078	.031		
6	.010	.020	.013	.059	.070	.062		
7	.010	.007	.004	.020	.026	—		
8	—	.002		.040	.035	.031		
9	.002	.002		.010	.035	—		
10				.020	—	—		
11				.010	.009	.031		
12				—	.009	—		
13				.010	—	—		
14				.010	—	—		
16				—	.009	—		
26				.010	—	—		
31				.010	—	—		

ences, show in the final period that the three types have retreated from the irritant in the order of their increasing number of taste buds, or in order of the nasal capsule changes, if such be considered as positive. Herrick (1903) showed that the delicacy of the sense of taste was directly propor-

tional to the number of taste buds in a given area. He worked on a variety of teleosts, including *Ameiurus*.

The anosmic specimens clearly did not avoid the irritant to nearly as great an extent as did the normals. It would thus appear that such avoiding reactions are

TABLE X. DIFFERENCE BETWEEN OBSERVED SEQUENCES AND BINOMIAL DISTRIBUTION.

These values obtained by subtracting the binomial distribution values of Table IX from the observed distribution of fishes from the same table.

SEQUENCE OF FISHES	RIV.	CHICA (2)	SAB.	ANOS.	RIV.	CHICA (1 - 3)	SAB.	ANOS.
1	.000	.000	.000	.000	.000	.000	.000	.000
2	.047	.067	.010	.101	.144	.182	.102	.435
3	.019	.077	— .010	.047	.081	.091	.098	.210
4	.021	.043	.001	.075	.036	.042	.033	.195
5	.006	.024	.008	.108	.009	.014	.023	.074
6	.010	.003	.003	.052	.002	.019	.019	.069
7	— .001	.009	.007	.027		.008	.007	.026
8	—	.007	—	.039		.008	.002	.035
9	—	.005	.002	.010		.002	.002	.035
10	—			.020		.002		—
11	.005			.010		.002		.009
12	.002			—		—		.009
13				.010		.001		—
14				.010		—		—
16				—		—		.009
24				—		.001		
26				.010				
31				.010				

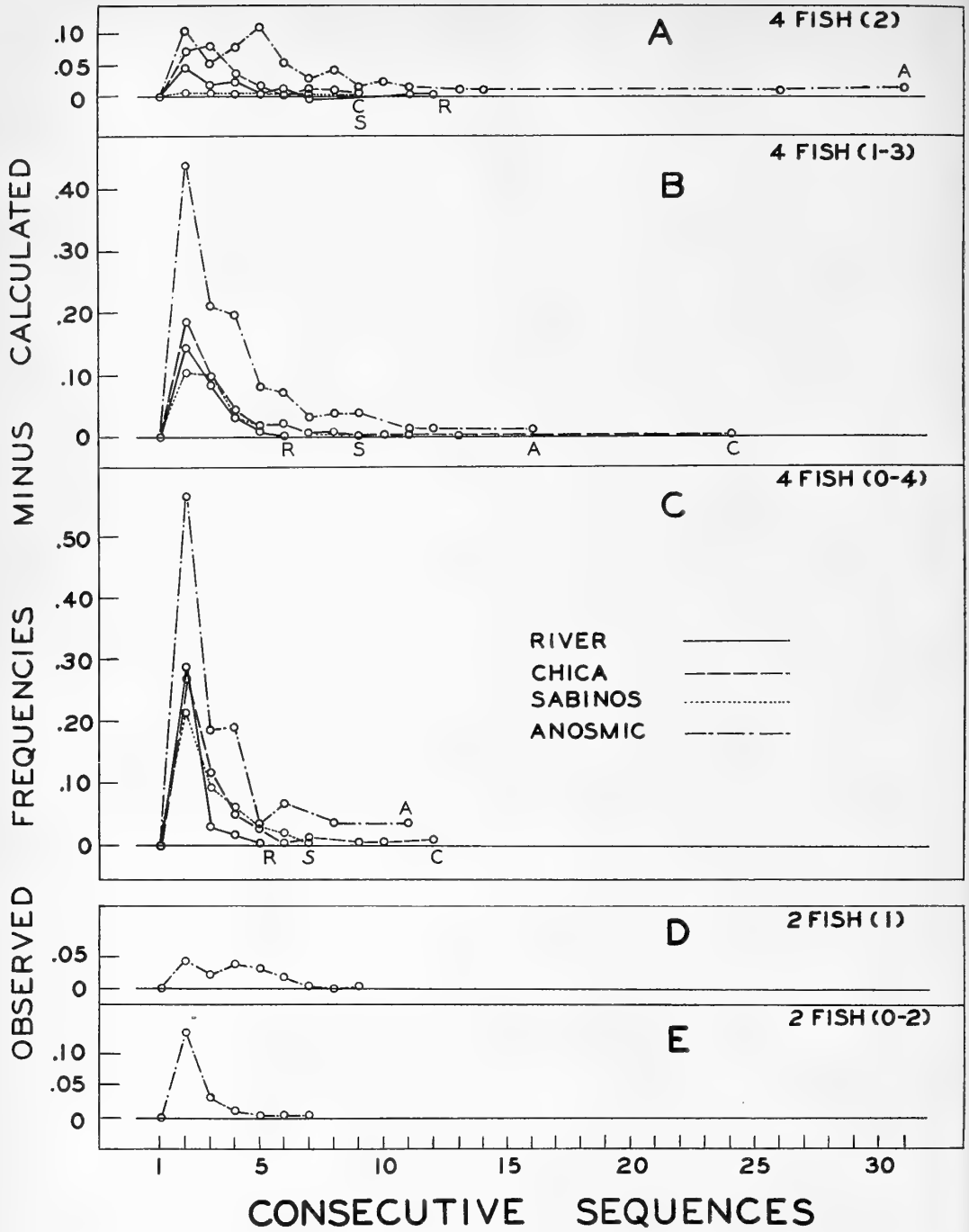
		ANOSMICS	
	(0 - 4)	(1)	(0 - 2)
1	.000	.000	.000
2	.289	.042	.139
3	.029	.018	.031
4	.014	.039	.008
5	.005	.033	.002
6		.016	.001
7		.002	.002
8		.000	
9	.003	.002	
10	.003		
11	—		
12	.006		

largely mediated by way of the olfactory apparatus. This could lead to the conclusion that the difference shown in graph B of Text-figure 3 (26 per cent., considering the range of from 0 to 50 as 100 per cent.) is a measure of the extent of the directive utility of the taste buds and the common chemical sense alone. The exact method of operation could be considered as occurring in two possible fashions. One would be that such chemical irritation is largely nasal and the other would be that the nature of the sensory perception is unimportant, but that part of it which happens to be nasal gave a much greater discriminatory ability with the consequence that the fish were able to react with more markedly appropriate action. One would hardly expect the range-finding ability of the diffuse taste bud and common chemical sense systems to be as accurate in locating the focus of a diffusing irritant as the discrete bilaterally paired nasal organs, even if the sensation in them were of a minute order. Expressed another way, retreat from an irritant is possible on taste and skin irritation alone but not with nearly as great accuracy as with the advantage of the more certainly directive nasal organs. It has already been indicated

by Parker (1922 and earlier) that the common chemical sense endings are stimulated by acid but these workers did not undertake to show how directive this response might be without the orientating nasal mechanism.

About all that can be said concerning the repellent characteristics of ammonium carbonate is that it is evidently much less of an item to be avoided than acetic acid in the same percentage solution. From these experiments it would be pointless to consider the relative ionization of the two substances in aquarium water with its mixtures of organic materials. Much further elaborate work involving the chemistry of the whole matter would have to be done in order to attempt to equate comparative effects of cation and anions, which is certainly only a small part of the entire matter, and in any case beyond our present province.

It is to be noted that there was some evidence of the fishes being at first slightly attracted to both the acid and the base. This is indicated in Text-figure 3, graph C and Table IV. In the case of the ammonium carbonate it is very marked and was noted during the progress of this experiment, for



TEXT-FIG. 8. Comparison of observed consecutive sequences of groups of fishes with distribution of probabilities of  $p^n$ . Based on the data of Tables VII, VIII, IX and X. Graphs A, B and C represent the data from experiments 1 and 7, river fish; 2, 5, 8 and 9, La Cueva Chica fish; 4 and 11, Cueva de los Sabinos fish; 3, anosmic fish. Graphs D and E represent the data from experiment 10, anosmic fish. See tables and text for full explanation.

in the early part of the dripping period the fish clearly gathered about the inflow at some point of evident equal concentration and were then pushed outward as this line of equi-potential moved forward. Actually it was first thought that this substance would have to be listed as an attractant and it is possible that it should be considered such in certain low concentrations. Normal eyed goldfish were used as a check on this item, the details of which are given in Table I, experiment 6, but not shown in Text-figure 3. Two additional periods, 9 and 10, not given in Table I, had values of 27 and 37 respectively. It is thus apparent from these data that the figures for the goldfish, from equality of distribution, rose sharply in the dripping period to very high values, 56 and 76, and then fell immediately to low values, 36, 32, 27 and 37, giving means of paired periods of 34 and 32. This is evidently merely an exaggeration of the conditions found in the characins. This may mean that goldfish are simply more reactive to ammonium carbonate as compared with the characins or that, since they were using visual cues and are a strongly aggregating species, any response would give the appearance of greater reaction because of the group tending to follow any individual that moves out from the aggregation. During this experiment one each of the following species were also present in the trough, but not counted: *Danio malabaricus* (Jerdon) *Lebistes reticulatus* (Peters), *Xiphophorus hellerii* Heckel, *Betta splendens* Regan and *Tilapia macrocephala* (Bleeker). These, while not aggregating with the *Carassius auratus* (Linnaeus), clearly showed similar behavior. It thus seems evident that certain low concentrations of ammonium exert an attractive influence at first and subsequently act as a repellent. Although somewhat masked in the graphs it was evident during the observations that the acetic acid acted in a similar fashion for a very brief period. This would seem to indicate that these and probably most fishes move toward practically any weak stimulus at first and then retreat from it if found noxious. This is evidently true of sound and mechanical shock as mentioned by Breder (1942).

The use of cane sugar as an attractant was established after various food juices, such as solutions of prepared dried food, horse meat extract and tubifex worm extract had been used and were found to exert no greater influence, as has been already noted. The others were abandoned for these tests because of technical difficulties in standardizing their quantities. Sheldon (1909) showed that while an elasmobranch, *Mustelus*, was generally sensitive to acids and alkalies in very dilute solution and less so to salts and bitter substances, they did not react to sugars, a feature certainly not

common to teleosts in general. For example, Trudel (1929) shows clearly that *Phoxinus laevis* Agassiz reacts to various sugars and indicates that the taste thresholds are, for the most part, not vastly different than in man. Krinner (1934) reviews the reactions of teleosts to NaCl. As noted in another connection, Strieck (1924 and 1925) has shown the interrelation of the sense of olfaction and taste in fishes. The characins under study, as has been indicated in the various tests, are evidently about as reactive to cane sugar as they are to meat juices and other possible food substances. This is evidently not so clearly the case, on the basis of the work of others, with different species of fishes. Kuroda (1932) has shown, by measuring changes in the respiratory behavior of *Ophiocephalus argus* Cantor, that sweet, sour, bitter and saline substances each induce a distinguishably different type of respiratory modification. This work was done on fishes held in a fixed position so arranged that the movement of the operculum traced a line on a kymograph drum. The exact significance of the variations of these movements in response to solutions of various gustatory substances is not clear, but his work suggests the possibility that further study by such a method might prove of value in present connections. Due to the small size of these characins, a more delicate arrangement than that used by Kuroda was constructed which, while mechanically satisfactory, could not be used with these fish. It was found that the slightest touch on the operculum would cause the fish to change its respiratory behavior in such a fashion as to reduce the movement of the operculum, in reference to the contact, to such minute proportions that mechanical amplification was completely impracticable. Due to the large variety of ways in which these fish can manipulate their opercular and branchiostegal apparatus, it was found impossible to so truss them up as to force them to make use of opercular movements against even the most delicate contact.

In addition to the interference of incidental influences inherent in the use of an attractant by such methods already mentioned, it must be borne in mind that fishes generally show notably rapid learning or conditioning. These specimens would go through their normal feeding reactions at first and when, on not finding anything palpable, would give up trying to find food. If, on the other hand, they had been presented with food at this time, they would have fed and then retreated because of a satisfied appetite, which indicates one of the difficulties in such an approach. The complications and irregularities in these experiments are evident in Text-figure 4, graphs A and B. It is not until the material is consolidated as in graph C that a fair estimate

of the effects may be obtained, which differs clearly from the relatively clear cut results obtained when an irritant was used. Here it is evident that the river fish showed a gradually increasing interest in the sugary taste, but of slight order. The normal Cueva Chica fishes showed a much stronger positive reaction to the same concentration, 40 per cent., while not such a strong one to 20 per cent. The Cueva de los Sabinos material showed the sharpest reaction to the sugar drip but quickly lost interest. The anosmic fishes showed more of a reaction than did the river fish and finally nearly reached the level of the normals in the last period. This is in accord with the general observations on the anosmics, to the effect that they take a materially longer time to locate and complete their feeding. Whether olfaction is involved here or not would be hard to establish in other than the sense discussed in connection with the repellent effect of acetic acid on the anosmics.

The longer term effects of both acid and sugar are indicated in Text-figure 5. As the period of observations were separated by varying lengths of time, this chart has had a time scale incorporated in the abscissa and pH values are given at the various observation periods. In the two lines concerned with acid it will be noted that there was a tendency to return to the normal figure. La Cueva Chica material, however, never did reach the equality value, even after both sides of the trough had reached the same pH value and there was no longer any directive differential. This may be due to a memory of the location of the source of the irritant, as it has been shown that these normally blind fishes have a strong memory of the location of obstacles, as was indicated by Breder and Gresser (1941b). The blinded river fish, on the other hand, nearly reached equality before the pH values had become the same at both ends and as soon as it reached that value spent more time in what was initially the repellent end. Since these fish, up the time of blinding, were dependent to a large extent on visual cues, it is possible that they did not retain such a strong memory of the location of the irritant. At least they did not, during this same period, have the adroitness in avoiding obstacles that the blind fish showed. This final strong bias to the acid end of the trough may have, in fact, been largely a matter of complete confusion.

The long term analysis of reactions to sugar shows the loss of interest in what was at first an attractant and perhaps a final irritation to it. Naturally there was no pH change involved and it is assumed that there was complete dispersion of the sugar solution before the end of the experiments, on the basis of the behavior of the acid and the

mixing caused by the constantly moving fishes.

Another approach to this analysis is that of considering the circling motions which these fish regularly make in regard to a unilateral anosmic condition. Table V and Text-figure 6 give the data of these studies. It is evident from the latter, graph A, that the normal and completely anosmic fish turn substantially as many times right as they do left in the presence of sugar, food or with no stimulus. The unilateral anosmics, on the other hand, show a strong tendency to turn toward the side of the intact nostril. In graph B it will be seen that the actual number of turns of both anosmics and normals were about the same in the column of no stimuli. The latter make less turns for the sugar and still less for the food. As the number of turns possible was related to the length of duration of the experiment, this falling off is due to their stopping or swimming straight ahead while actually feeding. It will be noted that the anosmics did not slow their pace. The semi-anosmics, on the other hand, slowed their pace for the sugar while they sought the unfindable stimulus and greatly increased it for actual palpable food. In the latter case they were impelled to make turns to one side only, which slowed their actual food finding. The process of locating a food particle served to increase their gyrations, thus accounting for their large number of circles. For some reason, not altogether clear, they usually turned toward the side of the missing nostril when engaged in chewing their food. Possibly it was a momentary negative response to additional food odors while they were actually engaged in mouthing a particle. Adrian and Ludwig (1938), for example, found that in the oscillographic recording of nerve impulses from the nasal capsule of *Ameiurus*, "A period of stimulation which has produced a considerable discharge is usually followed by a period of inactivity lasting 5-20 sec. or more. During this period the organ is insensitive to a second stimulus and the normal resting activity is greatly reduced."

It appears that what have been here classified as "repellents" and "attractants" are actually not truly separable on a qualitative basis for it must be recalled that the attractants also, in long term experiments, eventually exerted a repelling influence, while the repellents exerted an initial attraction. Stated in general terms the basic reaction would seem to be to move or turn toward any stimulus and then retire from it, irrespective of whether it be noxious or beneficial. The extent of the approach and retreat and the change in reaction in point of time would then be conditioned by (1) the specific attitude and physiological con-

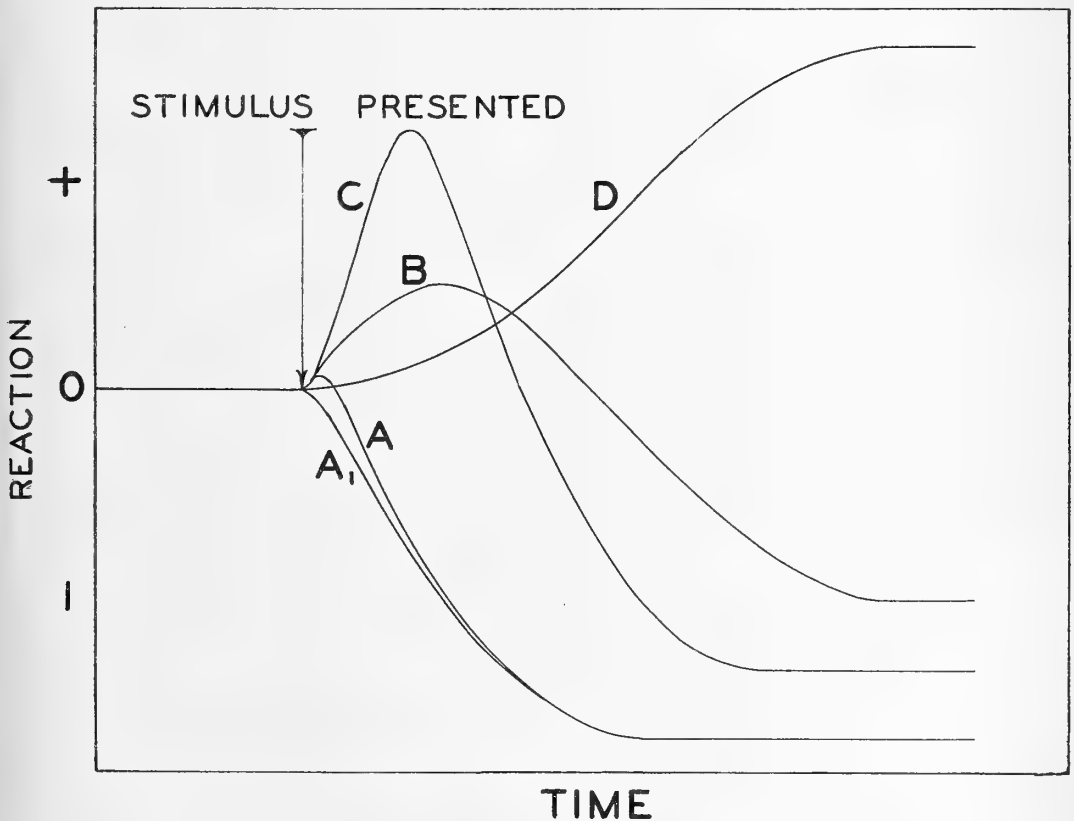


dition of the fish, (2) the violence of the stimulus and, (3) the chemical and physical nature of the stimulus. Considered in this manner, then, the various and superficially different behavior items in fishes in such a regard may be discussed in the following terms.

If the stimulus be sufficiently violent and sudden, as in the case of a heavy jolt, the positive reaction may be reduced to nearly or actually zero, an immediate retreat being all that is detectable. Anything short of such an item should then show an early turning toward or moving toward the stimulus, such as found in these experiments, followed by a retreat, the time and violence of which would be conditioned by the three characteristics listed above. In any case it is well known that the violence of both mechanical and chemical stimuli determines whether the reaction will be positive or negative. Parker and Van Heusen (1917) showed it very clearly for electrical stimuli as well. This would follow even if the stimulus were food which was found and eaten.

Probably only in the case of multiple factors would a permanent shift be obtained, which in its effects would practically amount to those involved in initiating a migration. The causes of movement in or out of a cave, as discussed by Breder and Gresser (1941b), would be of such a nature.

Text-figure 9 represents graphically an idealized concept of this general proposition. Much more work, not appropriate to the present paper, must be done to test thoroughly the validity of this view. Obviously any line, in addition to those hypothetical ones shown, could be drawn on such a chart. Those indicated, as based on present data and on general considerations, would seem to be some which do approximate reality. For example it seems that there is little likelihood of a line rising from the zero mark that would simply return to it and not show a movement to the negative side. After a reaction, obviously the lines would not remain horizontal, as shown, for an indefinite period. They would sooner or later return to the zero level (by



TEXT-FIG. 9. Hypothetical diagram of the quantitative nature of reactions to various stimuli. A, A<sub>1</sub>: stimuli in which a positive reaction is practically or completely absent. B: mild stimuli showing a slight attraction and subsequent repulsion. C: strong stimuli showing a marked attraction and a subsequent strong repulsion. D: a mild but permanent strong attraction. See text for full explanation.

a process of integration?) when a balance was once more established due to neutralization of the stimulus, its failure to give continuing directive effect, accommodation of the fishes or other matters, except in cases of the permanent establishment of a bias, where, as noted above, the permanent shift of a population would be involved.

This concept could be extended to include such cases where a fish retreats rapidly before a sudden splash and then later returns to the site of the disturbance, which apparently happens when the shock of the fright has fallen to a level where it is no longer a repellent.

In the development of an increased number of surface taste buds in this series of fishes the evolutionary changes involved are a little difficult to visualize. If one takes the selectionist view point and ascribes a selective advantage to the fish possessing a few more taste buds one would have to assume a restricted food supply. Such a condition does not obtain at present in La Cueva Chica where the bottom is floored with food substances, Breder (1942). Cut off from such a situation, dependent on a population of bats, a condition of limited food could be fairly considered but it is hard to see how a few more taste buds could be of much practical significance to the owner. Due to the continual random swimming of the species, each fish in time would cover all the area and the advantage of the better equipped fish would have to be on the basis that it covered a little wider "ribbon" or simply missed less food particles, a matter to be significant certainly calling for a fair increase in number of taste buds before selection could be expected to operate. Since the development of taste buds is evidently dependent on nerves developing first, Olmsted (1920), May (1925) and Torrey (1936), selection would apparently thus have to operate on cutaneous branches of gustatory nerves. Since the development of a new single branch would certainly call for the development of more than one taste bud, presumably at least several, it may be that a superficially slight neurological change would call forth a selectively significant increase in the number of taste buds.

Before the increase in the number of taste buds had been determined, Breder (1943) wrote, "... it may well be that these two blind populations are independent developments from the same basic stock and differ only in the accidental assortment of genotypes that gave rise to them." The intermediate nature of the taste bud tracts and the nasal structures, as well as other physical details not concerned with the present study would certainly seem to suggest that the Cueva Chica stock does in truth represent a stage in the evolution of the Cueva de los Sabinos population rather

than that the two forms represent independent but parallel developments. In this same paper it is stated, "The chemical senses are apparently normally developed in these fish, but do not seem to be hypertrophied. They show positive and negative reactions similar to those of various surface fishes," and "Histological examination shows no significant structural modifications in the fish from either cave." Also, "Thus, as far as present evidence goes, at least, we have a case of an intrusion into a 'simpler' environment with a loss of sensory refinements but with no evident substitute structural developments." The subsequent work, reported herewith, clearly changes the aspect of some of these statements for while it is still true that no histological or gross morphological changes have appeared, nor is there any evidence of a hypertrophy of the chemical senses, there are small morphological changes in the nasal capsule and changes in the number of external taste buds, at least the latter coming under the head of a positive change.

Considering the analysis of the distribution of the fishes during the control periods, some curious features appear. Regarding the distribution of the four types of fishes studied, it is clear from the tables and graphs that the river fish and those from Cueva de los Sabinos resembled each other in the behavior so expressed more closely than did the others. Also these two departed least from the expected distribution and their values are scarcely over the limits of statistical significance. The Cueva Chica fishes showed a greater departure from the expected distribution and when deprived of the sense of smell developed a still larger difference. This fact, coupled with the conditions noted during the observation periods in which the river and Cueva de los Sabinos fish appeared to be more cognizant of each other than did the rest, would seem to be difficult to reconcile. Thus if the data are tabulated by order of the tendency to aggregate, entirely contrary evidence is obtained between the visual impressions and the statistical treatment, as indicated below.

FISH	ORDER OF MAGNITUDE OF AGGREGATING TENDENCY	
	Statistical analysis	Visual impressions
Blinded river fish	1	3
Cueva de los Sabinos	1	3
La Cueva Chica	2	2
Anosmic	3	1

Disregarding for the present that the above two series of orders of magnitude are inverse, certain properties are common to each. The river fish and Cueva de los Sabinos fish are alike in both columns, the anosmics are at the other extreme and La Cueva Chica fishes are intermediate between them and the first two. Considering first only this feature of the tabulation, it should,

no doubt, be expected that the specimens deprived of the sense of smell would be set apart from the rest, as they are. Since La Cueva Chica material has been shown to be intermediate between the river fish and those from Cueva de los Sabinos in many ways, it is difficult to see why in the present respect the two end terms of the series are alike. Since the river fish, up to the time of blinding, showed strong aggregating tendencies based on acute vision, it may be that they employed some undetected mechanism used at night or in muddy water for the recognition of each other. This mechanism may be no different than that possessed by La Cueva Chica fishes, but the river fish may have simply paid more attention to each other through the same mechanism, because of past conditioning. The fish from Cueva de los Sabinos, on this basis, may have this, or some other mechanism, developing along with their taste bud and nasal changes so that they show similar behavior.

However one may wish to interpret these data it would seem clear that the sense of smell is involved in some manner, as is evidenced by the great difference in behavior of the anosmic fishes. Frisch (1938, 1941a and b) and Göz (1941) have shown that *Phoxinus laevis*, *Ameiurus nebulosus* (LeSueur) and *Alburnus bipunctatus* (Bloch) secrete a substance which can be detected by their fellows. Positive reactions are shown toward such materials (skin extracts) but retreat is shown to similar extracts of *Esox*, *Perca* and *Salmo*. In some cases individual recognition appears possible. Juices from an injured *Phoxinus* cause alarm in a school. These effects are apparently entirely olfactory. Hüttel (1941) discusses the chemistry involved. Bowen (1931) could not assign a role to olfaction in the aggregations of *Ameiurus melas* (Rafinesque). The present study is evidently the first to show by statistical methods that blind fish, both normals and operates, actually do demonstrate aggregating tendencies based on non-visual cues, and that measured by the standards of optically integrated groups it is a very feeble and loose structure. A considerable list of species and references to the visual nature of fish schools and aggregations is given by Breder and Nigrelli (1938). See also Shlaifer (1942). It is entirely possible that in any or all of these species a similar mechanism exists, for none of the work on the subject has been carried into such statistical analysis as the present. In all, the schools are simply broken up with a coming of darkness, while actually the disrupted schools certainly could not superficially show any less of an aggregation than did some of the present specimens. See, for example, Parr (1927) or Breder and Nigrelli (1935). In addition to the sense of smell being evi-

dently involved, the role of the lateral line, taste buds or other items is still to be explored.

It is of interest to note in this connection that Hoagland (1933) by oscillographic recordings of nerve impulses found that tactile stimuli to the barbels of *Ameiurus* gave large responses but that those from chemicals, such as acetic acid up to 20 per cent. solutions, 10 per cent. solution of NaCl and saturated sugar solutions gave scarcely detectable responses. He found that these tactile responses could be elicited by slight movements of the water. This condition may account for the relatively slight responses obtained with our chemicals and may indicate a truly large significance in regard to water movements. Breder and Gresser (1941a and b) have already established the large significance of rheotropic effects in these fishes which, except in the eyed river fish, cannot be optical in the sense shown by Lyon (1905, 1909a and b) and Loeb (1918) but are presumably akin to the tactile reactions such as those discussed by Jordan (1917) and Maxwell (1921a and b).

The puzzling inversion between the statistical analysis and the visual impressions is partly explained at an earlier place. It should be recalled that these measurements were made in a trough of two equal divisions and any fish was noted as either in or out of the compartment being checked. Thus the fishes might be close together or relatively far apart and still be counted in the one compartment, or, on the other hand relatively close together but counted as one in and one out. Actually this did occur in the case of the Cueva de los Sabinos fishes, for in several cases they tended to spend considerable time near the middle of the trough, evidently paying some attention to each other. Contrariwise it was not uncommon for the fish to spend a considerable amount of time running the circuit of the periphery of the trough. The fact that the river fish and the Cueva de los Sabinos fish did relatively little of this, spending more time in the central portion of the trough, certainly contributed to the impression that they were more cognizant of each other. This difference in behavior in itself very likely could be taken as a further measure of their tendency to awareness of each other, on the basis of the work of Breder and Nigrelli (1938) who showed that a solitary goldfish spent most of its time around the periphery of an aquarium and that a conveniently sized group spent most of their time at its more central parts. Obviously this change in behavior would not be reflected in the statistical analysis in a simple fashion. Thus the two inverse orders of magnitude between statistical measure and visual impressions may be reconciled on the

following basis. Because the river fish and the Cueva de los Sabinos specimens spent more time in the middle of the trough they appeared to be paying more attention to each other than to the periphery of the trough, and, evidently they were, but statistically they frequently split their group over the dividing line, thus failing to give the long and numerous sequences of a single group found in the others. The Cueva Chica material, spending so much time circumnavigating the trough, with attention to each other subsidiary, when once close together tended to stay that way to a greater degree. When these fish were made anosmic their basic behavior continued the same but not impinged upon by olfactory stimuli and guided, chemically, only by taste, their behavior appeared more deliberate and they seemed to show an exaggeration of the conditions found in them before becoming anosmic. The statistical values taken alone could be interpreted as meaning that the loss of the sense of smell made it possible for these fishes to detect each other more readily, certainly a ridiculous conclusion. Evidently, on the other hand, when they did locate each other, they tended to remain in company for longer periods than any of the others, either because of tasting each other, because of water movements or other unknown effects, or because of tending to move at a more uniform rate, not being impinged upon by the sharply bilateral nasal sensations.

That the nasal organs of fishes are comparable with those of terrestrial vertebrates and are used primarily as distance receptors for chemical entities as compared with taste buds and the common chemical sense, has long been established by a number of students. Reference to the bibliographies of the following will give a full history of the subject: Parker (1910, 1911, 1914 and 1922), Parker and Sheldon (1913), Sheldon (1911), and Olmsted (1918) together with many of the other references here mentioned in other connections. These workers concerned themselves chiefly with *Mustelus*, *Ameiurus* and *Fundulus*.

Experiment 6, on five goldfish, only referred to in connection with the discussion of the ammonium carbonate experiments, shows a marked difference from the behavior of any of the characin experiments in regard to present items of distribution. Both the distribution of the aggregations, Table VI, and the distribution of the sequences, Table VII, are inverted in respect to the characins. In both, the end terms are high and the central terms low. These fish had their full vision and seemed to be bothered by both the shallowness of the water and the fact that there was no cover whatever. The five of them were much more apt to be huddled together at one end or the

other as is indicated by the value of 27 per cent. for five and 27 per cent. for zero descending to 12 per cent. for 2 fish and 7 per cent. for 3 fish, the condition showing the greatest amount of dispersion. This clearly is not binomial distribution but rather an approximation of its reciprocal. It was for reasons such as this that it was necessary to blind the river fish, because of their extreme nervousness, in this case amounting to their jumping out of the trough. This is one reason that the relatively placid goldfish was used. It is interesting to note that the evidently highly exciting optical stimuli are apparently entirely responsible for the nervous condition of the river fish, for as remarked earlier, on being blinded, their general behavior becomes that of the cave fish, which is one of relative stability.

It has been shown in the earlier papers of this series that the evolution displayed by these fishes in retreating into a cave environment has involved losses, as follows: pigmentation, vision and ear structure. The present study shows that along with those losses there has been a concomitant gain in taste, while olfaction may eventually fall as either a gain or a loss. Although there is structural modification of the nasal capsule, behavior changes are evidently not great enough to be clearly measurable by the methods of the present studies on sensory response.

The blinded river fish, quite evidently little disturbed by their new condition, displayed the darkest color phase of which the species is apparently capable. The range of color change in these fishes is not great, but the behavior in this respect was typical of fishes in general on the loss of vision, see for example Odiorne (1937) who discusses similar color changes in blinded *Ameiurus*. The taking on of the wandering movements of the cave fish was not exactly expected, since other fishes such as trouts and sunfishes tend more to "sulk" in a corner under similar circumstances. This could mean that in spite of the large optical control evident in these river fish, they may be more active at night than one would ordinarily suppose. If this be true it would be another factor encouraging original cave entry. In any case Breder and Gresser (1941b) have indicated that these fishes show no hesitancy to enter dark places on slight encouragement. Evidently they are constitutionally so disposed.

#### SUMMARY.

1. There is a notable increase in the number of taste buds on the head and body from the normal-eyed river fish to the blind fish of La Cueva Chica and a still further increase to the more advanced fish from Cueva de los Sabinos.

2. In the same series and in like order the nasal capsules become more shallow and open but show a reduction in the number of sensory lamellae and consequently in the extent of sensitive epithelium. This is accompanied by an increase in the development of the directive nasal flaps.

3. The first positive development in the evolution of this series is shown to be in the taste mechanism and perhaps also in the olfactory mechanism, other sensory apparatus thus far studied having all shown reductive changes.

4. Avoidance reactions to chemical repellents is substantially the same for all three types, with a possible slight increase in sensitivity from the river fish to the more advanced cave forms.

5. Attention to chemical attractants is similar but not as well marked or differentiated.

6. Anosmic specimens avoid repellents not nearly as well as those with nostrils and take longer to locate attractants, evidently taste alone offering inferior orientation.

7. Fatigue, confusion or distress, any or all, neutralize and may tend to invert the negative or positive reactions in one to three hours.

8. Semi-anosmic fish show a strong bias to turn toward the side of the functional nostril, with stimuli either present or absent, indicating the orientation control to be largely nasal in these fishes.

9. The primary nature of reactions to either noxious or beneficial stimuli is suggested as being basically the same, differing only in a quantitative sense.

10. Non-visual influences concerned with the limited aggregating tendency of these fishes evidently involves the nasal capsule, in part at least, for anosmic specimens showed behavior different from the others.

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## EXPLANATION OF THE PLATES.

### PLATE I.

Comparison of nares in Mexican characins.

UPPER: from Rio Tampaon, 45 mm. in standard length.

MIDDLE: from La Cueva Chica, 52 mm. in standard length.

LOWER: from Cueva de los Sabinos, 51 mm. in standard length.

### PLATE II.

Comparison of nasal capsules in Mexican characins.

UPPER: from Rio Tampaon, 34 mm. in standard length.

MIDDLE: from La Cueva Chica, 29 mm. in standard length.

LOWER: from Cueva de los Sabinos, 32 mm. in standard length.

Each section represents a transverse cut through the posterior nostril in a homologous region, median side to to the right. Compare with Text-figure 1 for location of these sections and their interpretation. Magnification 57.5  $\times$ .

### PLATE III.

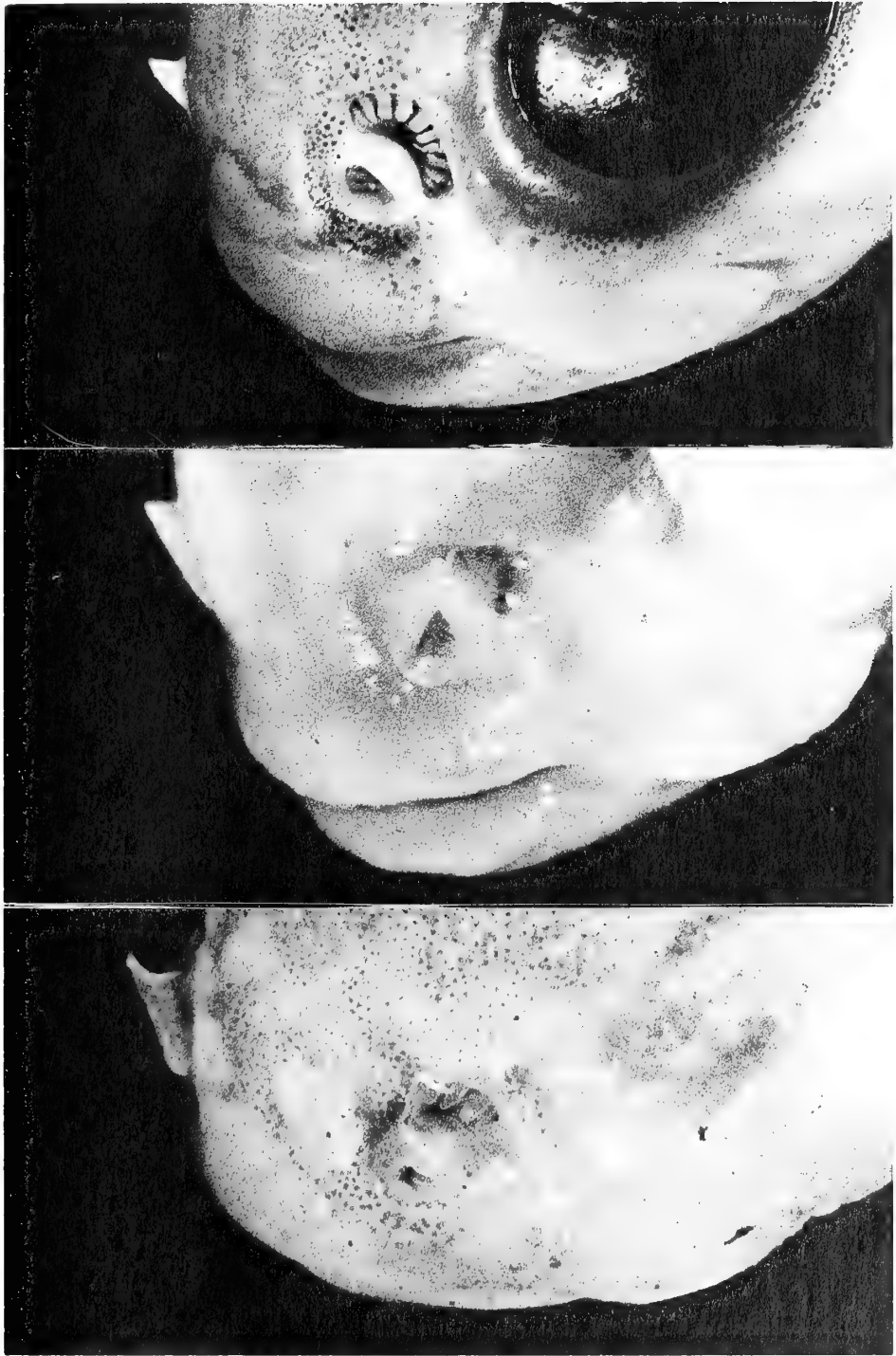
Comparison of taste buds from various regions of the body from a La Cueva Chica specimen of 29 mm. in standard length.

UPPER: from interior of buccal cavity.

MIDDLE: from exterior of head.

LOWER: from lateral portion of body. The dark layer at the lower part of this photograph represents a scale. See text for full explanation and Text-figure 2 for the distribution of these organs. Magnification 695.5  $\times$ .





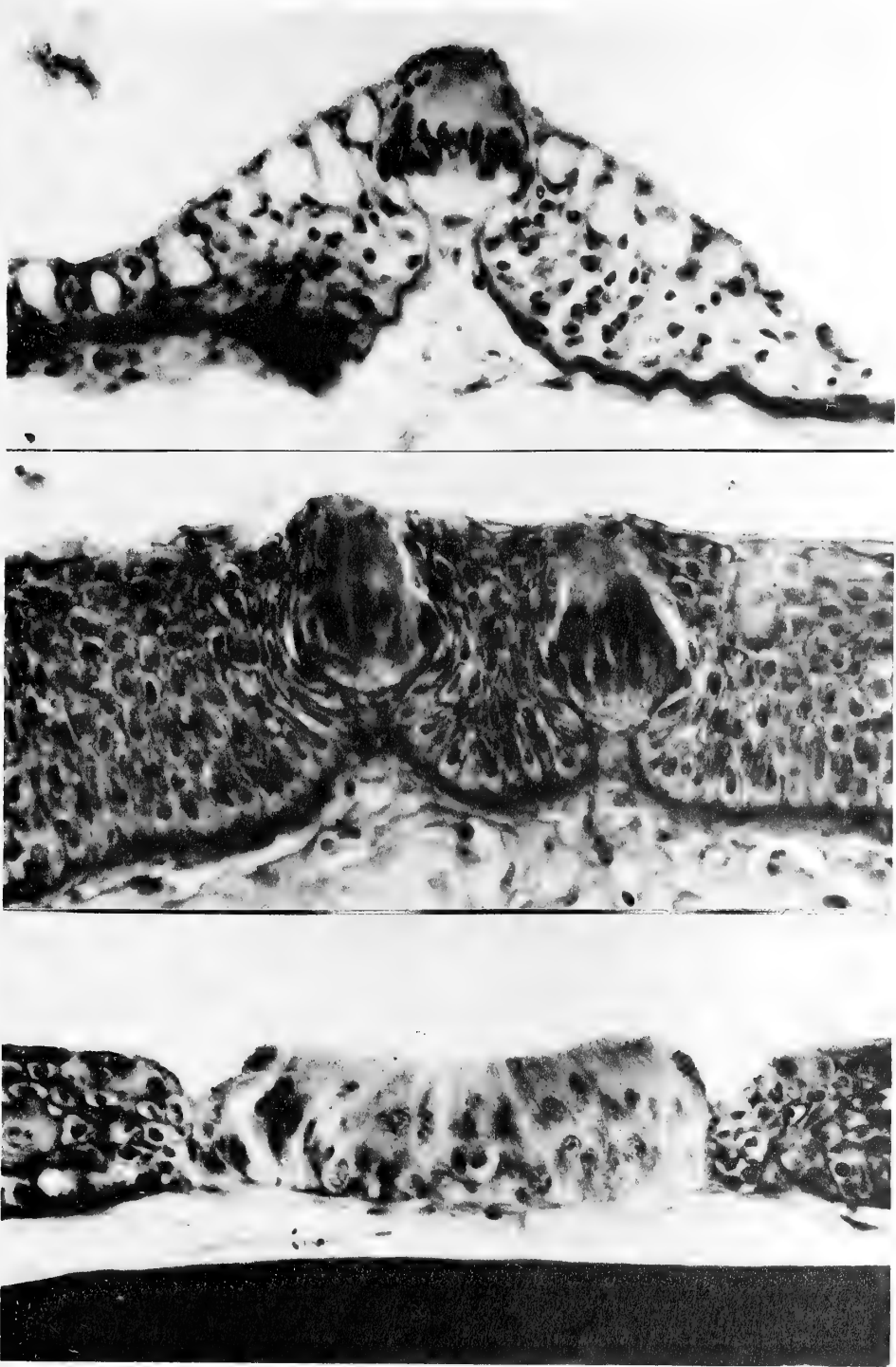
CHEMICAL SENSORY REACTIONS IN THE MEXICAN BLIND CHARACINS.





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## 21.

The Avian Genus *Zosterops* in Siam, with Description of One New Race.

H. G. DEIGNAN.\*

Recent revisional studies of the white-eyes of the Asiatic mainland have either (through scarcity of suitable material) given the impression that the genus stopped short at the eastern confines of the Indian Empire or (for the same reason combined with a lack of knowledge of Siamese zoögeography) have handed down opinions on distribution and nomenclature at variance with the apparent facts. My own investigations lead me to recognize in Siam four species, one of which (*palpebrosa*) is represented by no less than four geographical races:

1. *Zosterops erythropleura* Swinhoe.

*Zosterops erythropleura* Swinhoe, *Proc. Zool. Soc. London*, August, 1863, pp. 204, 298 (Shanghai, China).

A very uncommon winter visitor to northern Siam, where it has been recorded only from Doi Su:thep, Doi Chieng Dao, and Phu Kha, at elevations between 4,500 and 5,500 feet; the extreme dates for its stay are 7 November (1936) on Doi Su:thep and 7 April (1936) on Phu Kha.

2. *Zosterops japonica simplex* Swinhoe.

*Zosterops simplex* Swinhoe, *Ibis*, July, 1863, pp. 294-295 ("Southern China, from Canton to Foochow").

An uncommon or locally common winter visitor to the northern provinces of Chiang-mai, Lampang, and Chiangrai, recorded between 9 November (1930) on Doi Langka and 1 March (1933) on Doi Su:thep; it is chiefly a bird of the plains but has been taken on Doi Chieng Dao at 4,500 feet (2), on Doi Su:thep at 5,500 feet (1), and on Doi Pha Hom Pok at 6,400 feet (1).

3. *Zosterops palpebrosa mesoxantha* Salvadori.

*Zosterops mesoxantha* Salvadori, *Ann. Mus. Civ. St. Nat. Genova*, ser. 2, vol. 7, 1889, p. 396 (Tahoe, Karen-ni).

*Zosterops palpebrosa vicina* Riley, *Proc. Biol. Soc. Washington*, vol. 42, 1929, p. 162 (Doi Su:thep, North Siam).

A common permanent resident on those hills of the Tha:non Thong Chai and Khun Tan chains (with the exception of Doi Nang Keo?) which reach elevations in excess of 4,500 feet; on Doi Pha Hom Pok it ranges up to 6,000 feet and, on Doi Su:thep, has often been seen as low as 3,300 feet. Probably owing to the insufficient altitude, it has never been recorded from Doi Khun Tan by any one of the numerous collectors who have visited that mountain.

Our bird is neither *palpebrosa* (Bengal), which has the underparts vinaceous-ashy and the mesial streak of exceptional occurrence, nor is it *auriventer* (Tavoy), a coastal form which has the mesial streak broader and brighter and the retrices almost without olive-green edging.

4. *Zosterops palpebrosa joannae* La Touche.

*Zosterops aureiventer joannae* La Touche, *Bull. Brit. Orn. Club*, vol. 42, 1921, pp. 31-32 (Mengtz, S. E. Yunnan).

I place here two females taken by me on Doi Chieng Dao at 6,200 feet, 19 March, 1937; the two males and three females reported by Greenway (*Bull. Mus. Comp. Zool.*, 1940, p. 190) from Doi Nang Keo, 2,800 feet, 8-15 April, 1937 (examined); and, with reservations, a juvenal male from Phu Kha, 4,500 feet, 16 April, 1936. On Phu Kha, at the borders of Laos, it may well be the breeding race; to Doi Chieng Dao, where *mesoxantha* also occurs, it is merely a rare winter visitor; its status on Doi Nang Keo is unknown but, if it occurs only in winter, it is at least remarkable that not one of five specimens should belong to the resident form so common on the neighboring hills.

As quoted by Greenway (*loc. cit. supra*), Stresemann states, *in epist.*: "*Palpebrosa* from Mengtz, called *joannae* by La Touche, is very near to *mesoxantha* Salvadori, but has the flanks a slightly darker grey and the upperside more greenish, less yellowish. The name *joannae* may stand, therefore, but the racial characters are very feebly pronounced."

A white-eye, which may be *joannae*, occurs at all seasons in the lowland evergreen of Chiangrai province. My memory of certain specimens from Chiangrai-Town, in

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Sir Walter Williamson's collection, is that they agreed perfectly with my examples of *joannae* from the heights of Chieng Dao, but his birds were perhaps merely winter visitors. Three males taken by me at and near Wieng Pa Pao, 24 and 30 July, 1935, are more golden than any others seen and might be considered very worn *mesoxantha* but Salvadori's race is not otherwise known in Siam from so low an elevation and there is a strong possibility that *joannae* in the same state of wear would show an equally golden hue. Because of these doubtful points and the uncertain status of *joannae* on the nearby Doi Nang Keo, it seems best to leave them for the present without subspecific determination.

5. *Zosterops palpebroso williamsoni*  
Robinson & Boden Kloss.

*Zosterops palpebroso williamsoni* Robinson & Boden Kloss, *Journ. Nat. Hist. Soc. Siam*, vol. 3, 1919, p. 445 (Me Klong, Central Siam).

A resident of the western littoral of the Siamese Gulf, ranging along the eastern shore of the Malay Peninsula from Bangkok to Pattani.

6. *Zosterops palpebroso auriventer* Hume.

[*Zosterops*] *auriventer* Hume, *Stray Feathers*, vol. 6, 1878, p. 519 (Tavoy).

A littoral form, resident along the western shore of the Malay Peninsula and occurring on the coast and islands of Siam from Victoria Point to the Malay States.

*Auriventer* is separable from *williamsoni* by the rather deeper yellow of the throat and under tail-coverts, by the presence of a broad and distinct mesial streak (exceptional in *williamsoni* and then barely indicated),

and by having the rectrices virtually without olive-green edging.

In applying Hume's name to this bird, I follow the line of reasoning set forth by Stresemann (*Journ. f. Orn.*, vol. 87, 1939, p. 158, footnote 2).

Away from the coasts, in montane and submontane districts of the Siamese portion of the Malay Peninsula, is found a race of *Zosterops atricapilla* (cf. Stresemann, *loc. cit. supra*, pp. 159-160) quite distinct from *Z. a. tahanensis* Ogilvie Grant (Malay States), with which it has been heretofore confused. I suggest that it be called

*Zosterops atricapilla wetmorei*, subsp. nov.

Type: Adult male, U. S. Nat. Mus. no. 234322, collected at Chong, near Trang, Peninsular Siam, 5 December, 1909, by C. Boden Kloss.

A series of 8 adults of the new form from the type locality, Khao Nong (3,000-4,300 feet), Khao Luang (3,400 feet), and "Khao Bhanam Bencha" (3,500 feet) differ from a series of 6 of *tahanensis* (including 4 topotypes) by having the upper parts a brighter and much more golden olive-green and by having the bill as much longer than that of *tahanensis* as this part is longer in *tahanensis* than in *sumatrana*.

N. B. Despite its name, *Zosterops palpebroso siamensis* Blyth (Tenasserim) has never yet been noted within the borders of Siam, although it is evidently common at so near a locality as Mount Muleyit.

For the loan of valuable series of the birds here discussed, as well as of allied races, my cordial thanks are due the authorities of the American Museum of Natural History, of the Museum of Comparative Zoölogy, and of the Academy of Natural Sciences in Philadelphia.



## 22.

## Causes of Diseases and Death of Fishes in Captivity.

ROSS F. NIGRELLI.

Pathologist, New York Aquarium.

(Plates I-VI).

## INTRODUCTION.

This report deals with the several causes of mortality of fishes exhibited in The New York Aquarium at Battery Park, New York City. Attempts are made here to analyze the more important causes and to indicate, where possible, therapeutic and prophylactic measures. It is hoped that these records will be of some value in maintaining fish in good health and in preventing major losses.

The lists of causes of deaths for 1940 and for the first eight months in 1941 are shown in Tables I-III. It was soon after the latter date that the Aquarium closed its doors at the Battery and the fishes and other vertebrates and invertebrates were distributed to certain institutions or brought to the temporary Aquarium in the New York Zoological Park.

The agents causing death of specimens in the present temporary Aquarium are few and will not be discussed in detail. It is sufficient to report that the number of mortalities for 1942 was exceptionally low and the causes limited to such factors as handling, temperature and chemical changes and to such pathogens as *Saprolegnia*, *Mycobacterium* and *Ichthyophthirius*.

It may be of interest to point out that the terminology used in designating the causes of death of fishes follows, as much as possible, the "Manual of the International List of Causes of Death" for human beings published by the United States Department of Commerce (1939).

## ANALYSIS OF THE IMMEDIATE CAUSES OF DEATH OF FISHES.

## I. GENERAL REMARKS.

Table IV gives comparative figures on the number of monthly mortalities for the years 1939, 1940 and for the first eight months of 1941. The saturation of the population density suddenly with large collections of fishes explains, in part, the quick rise in the number of deaths at any given time. In 1939, a large shipment of marine fishes was received from Florida and placed on exhibition. The devastating effect of this procedure is reflected in the great number

of losses shown for July and August of that year. No exceptional losses were incurred in 1940 and 1941, when only small shipments were received from time to time and the fishes were introduced gradually into the established population. Further, diseases that may have appeared were kept under control.

A similar picture can be demonstrated for the temperate fresh-water species. In 1939, collections of these forms were held down to a minimum, but when several big hauls were made in 1940, comprising mostly trout and other psychrophilic forms, parasitic diseases became rampant on the rise in temperature, and because of the crowded conditions, the high mortalities shown in June and July of that year were the result. When the susceptible fishes died off, the death rate once more approached the normal.

The steady death rate that is indicated for the tropical fresh-water fishes is accounted for by the fact that each tank is an independent system and diseases, therefore, are limited to the particular tank in which they appear. Furthermore, the population of these tanks is more carefully adjusted.

In general, there was a significant decrease (about 20%) in the total number of deaths among fishes in the Aquarium in 1940 as compared with the number of mortalities during 1939. Controlling the population density was the main factor in this decline.

Concomitant with the decrease in mortality was the increase in average longevity. The average life span in captivity was about 12 months in 1939, 15 months in 1940 and 17 months in 1941. A census taken in April, 1941, showed that 71% of the fishes on exhibition were under 2 years; 15% 2-5 years and 14% over 5 years.

II. CAUSES OF DEATH OF MARINE FISHES.  
(Table 1)

Among the marine species the decrease in mortalities was especially significant as shown in Table IV and, for the most part, is due to the almost complete disappearance

TABLE I.

## CAUSES OF DEATH OF MARINE FISHES.

## Parasitic and Infectious Diseases.

DISEASES	1940	1941
Diseases of Skin and Gills		
1. Bacterial	8	23
2. Oodinium (Flagellate)	11	—
3. Trichodina (Ciliate)	20	24
4. Myxosporidia (Cnidosporidia)	—	3
5. Epibdella (Trematoda)	99	2
6. Microcotyle (Trematoda)	44	14
7. Diplectanus (Trematoda)	2	—
8. Argulus (Copepoda)	2	—
9. Livonica (Isopoda)	1	—
Diseases of Skin and Internal Organs		
10. Lymphocystis	9	—
Diseases of Digestive System		
11. Enteritis and Stenosis due to Acanthocephala	5	5
Diseases of Circulatory System		
12. Pericarditis due to Echinostome infection	—	1
Total	201	72
Non-Infectious and Non-Parasitic Diseases.		
Neoplastic Diseases		
13. Nephroma	—	2
14. Thyroid Tumor	1	1
Diseases of Digestive System		
15. Prolapsed Intestine with Stenosis	1	—
16. Hepatic Degeneration	7	10
17. Fatty Degeneration of Liver	—	11
Diseases of Urinary System		
18. Kidney Degeneration	—	5

## Diseases of Reproductive System

19. Ovarian Degeneration — 1

## Diseases of Circulatory System

20. Cardiac Degeneration — 3

21. Fatty Degeneration of Heart — 1

22. Ruptured Myocardium 1 —

23. Gas Embolism (Cerebral Hemorrhage) 61 4

24. Internal Hemorrhage — 2

## Diseases of Bone and Organs of Locomotion

25. Tail atrophy — 1

## Diseases of Ill-defined Causes

26. General Degeneration of Internal Organs — 2

27. Edema — 1

## Violent and Accidental Deaths

28. Killed in Fighting 26 22

29. Jumped Tank 2 3

30. Fractured Skull 1 2

31. Multiple Abrasions 10 8

## Deaths Due to External Causes

32. Temperature Changes — 2

33. Changes in Water Chemistry 85 2

## Diseases of Organ of Vision

34. Blindness 9 1

## Diseases Due to Nutrition

35. Malnutrition 17 —

36. Fatty Degeneration 4 —

## Senility

37. Deaths Due to Old Age — 4

38. Causes Unknown 67 35

Total Non-infectious Diseases 292 123

Total Infectious Diseases 201 72

Grand total 493 195

of *Oodinium ocellatum*, a parasitic dinoflagellate, as an important death producing agent. This organism, together with another protozoan form, *Trichodina*, and the monogenetic fluke, *Epibdella melleni*, was responsible in 1939 for more than 60% of the deaths. In 1940, these parasites were the cause of only 26% of the fatalities. Although there was a decrease in the number of deaths due to *Epibdella* (Fig. 2) in 1940, it was still a major cause, being responsible for 20% of the mortalities; up 2% over the previous year. The decrease in the number of deaths resulting from *Epibdella* was partly due to the fact that epidemics of this form were controlled by limiting and segregating highly susceptible fishes, particularly the members of the family Chaetodontidae, and by a consistent application of prophylactic and therapeutic measures. The continuance of these measures (limiting the collection of susceptible fishes, control of temperature and density of sea water) yielded effective results with almost complete disappearance in 1941 of this agent as an important cause of death.

In spite of an increase in the number of mortalities due to *Microcotyle*, this fluke

was never a real threat because it failed at any time to reach epidemic proportions. The site of infestation is limited to the gills of a few species of chaetodontid fishes. Dipping infested fish in fresh-water of the same temperature as the sea water from which they were taken is a very effective treatment. In using this technique, care should be taken not to prolong the exposure to fresh-water beyond a certain time limit, which must be established for the various susceptible species.

It was stated by Ward (1908) that "the parasitic fauna is primarily a function of the habitat of the species" and that marine fishes (e. g., salmon) "carry their marine parasites with them into fresh water but soon lose them." It is this basic principle that is put into practical use above. In treating parasitized fresh-water fishes, sea-water is used in the same manner. This procedure is highly effective and with least danger to the host for those migratory species which move from fresh water to sea-water and back again (e. g., eel, trout, salmon, etc.).

Two species of *Trichodina* (*T. spheroides* Padnos and Nigrelli and *T. halli* P. and N.,

1942) were responsible for 10% of the deaths of marine fishes in 1939, 4% in 1940 and 12% in 1941. However, the 1941 deaths due to this peritrich ciliate were limited to puffers (*Sphaeroides maculatus*) which were segregated after it was determined that this host was the foci for deaths of other species. Nigrelli and Atz (1943) pointed out the importance of a routine check for parasites of fishes that are to become part of an established and healthy collection. The danger of introducing fish haphazardly was demonstrated strikingly when a routine examination revealed that the epidemic of trichodiniasis in 1939 had its origin in puffers taken from Sandy Hook Bay area. Oodiniasis also was centered in puffers and other fishes from this area (see Nigrelli, 1936). Knowledge of the principal host and the area from which the fish are taken becomes an important item in controlling disease-producing organisms that may destroy other and more important exhibition specimens.

#### A. OTHER CAUSES OF DEATH OF MARINE FISHES.

##### 1. Bacterial

A large gram-positive bacillus was found associated with certain skin lesions present on sea robins, toadfish and striped bass. In the latter, the rods were recovered from the kidneys. Externally, the lesion appears as whitish patches on the dorsal part of the body. When the growth becomes extensive death results. These fish are ordinarily placed in filtered bay water (low sp. gr. and pH) and the disease appears in about ten days after they are brought in from local waters. Similar species kept in the closed circulation (high sp. gr. and pH) did not show this infection.

An infectious dermatitis of similar type, but caused by a gram-negative bacillus, was reported by Zobell and Wells (1934) for several marine species of the west coast.

##### 2. Lymphocystis.

This disease, peculiar only to teleost fish, is of a much wider distribution than has been suspected. An intracellular virus is believed to be the causative agent and the lesions appear as nodular growths on the skin and fins of the host. Microscopically, the growth shows tremendously enlarged connective tissue cells. The real nature of this condition was first reported by Weissenberg in 1914 (see also Weissenberg, 1938) in certain European fishes. Lymphocystis was reported from marine fishes in the N. Y. Aquarium by Smith and Nigrelli (1937), Weissenberg, Nigrelli and Smith (1937), Nigrelli and Smith (1939) and by Nigrelli (1940). In these papers the following hosts were described as being affected: blue angelfish (*Angelichthys isabelita*), hog-

fish (*Lachnolaimus maximus*), orange filefish (*Ceratacanthus schoepfii*), and the clownfish (*Amphiprion percula*). The disease was not seen in 1941 but in 1940 nine cases were found in which the growth had invaded the internal organs, producing the identical lesions reported by Nigrelli and Smith (1939) for the orange filefish. The hosts involved in these cases are: orange filefish (*Ceratacanthus schoepfii*), banded butterflyfish (*Chaetodon striatus*), black angelfish (*Pomacanthus arcuatus*), and East Indian cowfish (*Ostracion cornutus*). In 1942, a cowfish (*Lactophrys tricornis*) sent to the writer by Dr. C. M. Breder from Palmetto Key, Florida, was found to be affected by this interesting cellular hypertrophy. However, it should be noted that this disease is by no means limited to marine fishes. It has been reported from fresh-water teleosts by other investigators and in the present report is listed as the cause of death of a red-spotted sunfish, *Lepomis humilis* (see Table II).

Among the writer's collection of diseased fishes are several specimens of striped sleepers (*Dormitator maculatus*) (Fig. 14) discovered by Dr. Myron Gordon on one of his trips into Mexico, and a number of pike-perch (*Stizostedion vitreum*) collected by Louis Krumholz from lakes of Illinois. Both species show extensive growths on various regions of the body. Further comparative histo-pathological studies are being made which will be prepared in detail for a later publication.

##### 3. Internal Parasites.

Fishes that die in captivity from internal metazoan parasites usually obtain the infestation in the feral state, since in practically every instance a specific transmitting agent is required. Molluscs and crustaceans are typical intermediate hosts necessary in the life-cycle and transmission of parasites such as digenetic trematodes, tapeworms and spiny-headed worms (*Acanthocephala*). Because of this fact, parasites belonging to these groups are easily controlled by the simple expedient of removing from the system suspicious intermediate hosts or vectors.

In general it may be said that fishes kept in captivity tend to lose their intestinal parasites after a short time, and these parasites cause little or no damage to the host tissues. Occasionally, however, the infestation may be heavy and the damage produced so extensive that death eventually results. Thus, five striped bass (*Roccus lineatus*) in 1940 and five in 1941 were found to be heavily parasitized with spiny-headed worms (*Echinorhynchus proteus*) (Fig. 3). The worms had perforated the intestinal wall. In some instances, the host tissues reacted to this infestation by walling off the parasite but in other cases the regenerating

tissue was so extensive that an intestinal stenosis developed.

#### 4. Physical and Chemical Factors.

These factors, together with nutrition, account for a large number of deaths among marine fishes and will be discussed again in this paper. Since the nature of these factors is for the most part known, the only criterion necessary to reduce deaths due to them is better management or better equipment. Some factors are beyond control; e. g., sudden increase in concentration of nitrogen gas which appears periodically in certain marine aquaria. The source of this gas is still a mystery. In 1941, gas embolisms were the cause of 61 fatalities of pilotfish, rudderfish, sea bass, croaker, common jack, etc. The condition first appears as extravasation of the surface capillaries, especially in the region of the fins. Exophthalmos is a later manifestation, the result of hemorrhages in the posterior chamber. Just before death, the affected fishes swim in gyrations, turn upside down and finally pass into coma. Examination of brains of these fishes shows cerebral hemorrhages and extensive infarctions (Fig. 4).

#### 5. Violent Deaths.

Fighting, jumping out of the tanks, banging snouts against the wall and glass of the aquaria invariably account for large numbers of mortalities. The interesting phenomenon of leaping demonstrated by tarpons (*Tarpon atlanticus*) resulted in 18 deaths in 1940 and 1941. These fish were sent to the Aquarium by Dr. Breder from Palmetto Key, Florida, when they were several inches long. After surviving the initial shock of handling and transportation, they became acclimatized to the aquarium conditions and in two years measured from 2 to 3½ feet. During this growth period the fish behaved quietly and only occasionally would they break the surface. Suddenly they began to take great leaps, banging their heads and backs on the cross beams supporting the large tanks which contained them. The multiple abrasions received resulted in death.

Schlaifer and Breder (1940) made a detailed study of leaping behavior of young tarpon under various conditions and pointed out that large temperature changes were the important factors involved in this respiratory activity. It is also known that increased density causes an increase in the respiratory rate (see Keys, 1931) in certain marine fishes. Whether this was a factor in inducing tarpon in the Aquarium to leap is not definitely known. At the time that the fish began to leap, the density of the sea-water had reached a specific gravity of 1.030 and when this density was reduced by the addition of fresh-water of same temper-

ature to 1.020 the fish became quiet. It is known that tarpon in fresh water also show the leaping behavior. It may be, as suggested by Dr. Breder, that the two extremes may produce an exhilarating effect, causing the tarpons to jump. Further studies of this behavior in relation to the tonicity of the environment may yield some interesting information.

#### 6. Diet.

In a large and varied collection, the problem of proper feeding is rather difficult. Certain fish require special diets which it is not always possible to obtain. A typical example is the case of seahorses. These interesting fish, with their peculiar mouths, can eat only small food and have a preference for minute crustaceans, such as *Gammarus*, brine shrimp, etc.

The comparatively high incidence of renal and hepatic degeneration is indicative of a faulty diet. There is much comparative evidence to show that such degenerations are involved in vitamin B-complex deficiency. This problem is referred to again in the summary of the factors contributing to major losses of the fishes in captivity.

On the other hand, confinement to relatively small tanks of more or less active fish tends to cause the fishes to lay down enormous amounts of fat. This condition is often found among the older captive fishes, especially those that have been in the tanks from five to ten years. Infiltration and degeneration of fat may occur in the liver, kidney and heart and was probably the cause of death in those specimens so affected.

#### 7. Neoplastic Disease.

Neoplasms of various sorts have been encountered among marine fishes. This item, however, is not as important as a cause of death as it is interesting in the light of similar diseases in humans and other mammals. In fishes, as in human beings, neoplasms are classified according to the tissues or cells involved. The etiological agents responsible for these growths are not always known but they may be due to virus, animal parasites (Neosporidians), heredity, presence or lack of certain chemicals. The nature of some of these fish tumors was reported by the writer (Nigrelli, 1937). Among the tumors, adenocarcinoma of the thyroid appears to be most common among captive fish. In 1940 the writer reported ten cases of thyroid tumor in the sheep-head minnow (*Cyprinodon variegatus*). This occurred spontaneously in an established school of fish in one of the tanks but no evidence was obtained to indicate the cause. One interesting case was found in 1940. The fish involved was a blue angelfish (*Angelichthys isabelita*) (Fig. 5) in which the thyroid tumor had grown deep into the

bronchial cavity with an involvement of gill tissues. Histologically, the structure presents a complex network of vascular stroma containing small alveoli without definite lumina and larger, mature alveoli with or without colloid.

#### B. SUMMARY OF CAUSES OF DEATH AMONG MARINE FISHES.

Table V summarizes in percentage the general causes of mortality among fishes in the Aquarium for the years 1939, 1940 and 1941. It will be seen that there is a sharp decrease from 1939 in the percentage of marine fishes affected by one or more infectious diseases. Concomitant with this decrease, however, was an increase in the percentage of non-infectious diseases, excluding violent deaths, deaths due to abnormal water conditions or unknown factors. Most of the non-infectious diseases occurred in fishes which have been on exhibition for more than one year, and are of the types, as may be seen in Table I, that one normally would expect to find among any animal population of similar proportions and under conditions of confinement.

#### III. CAUSES OF DEATH OF TEMPERATE FRESH-WATER FISHES.

(Table II).

Parasitic diseases took a heavy toll of temperate fresh-water species. This may be partly attributed to certain difficulties encountered with the closed circulation put into use for the first time in the early part of the summer of that year, and the fact that the system's population was suddenly increased by several new collections of cold-water fishes. As shown in Table V the percentage increase of parasitic and infectious diseases was not much greater than in 1939. The rise is due to the fact that physical factors of temperature and aeration were responsible for a significant increase in mortalities for 1940. As may be seen from Table IV the heavy mortalities took place in June and July. Returning the system to an open circulation, especially those tanks containing species requiring lower temperatures and high oxygen content, resulted in an immediate drop in the number of deaths.

The ciliate, *Ichthyophthirius*, as well as the trematode, *Urocleidus* (Gyrodactyl-oides), and the copepod, *Argulus*, were responsible for 47% of the deaths. These forms had reached epidemic proportions in 1940, and were active during the warmer months when the conditions of crowding and increased temperature were the prime factors in breaking down host resistance. The infestation started on fishes newly acquired in June and the epidemic raged in July with an increased virulency, killing

many of the older fishes (average age of 120 fishes, about 4 yrs.). Coincident with the epidemic was the fact that this was a period of abnormal temperatures, both for water and air. The water temperature (July 29) in the closed circulation had reached 77° F. as compared to 67° F. for the water in the open system. Certain fish that had survived the infestation were killed by this increased temperature.

The fishes most affected by the temperature changes were various species of trout, pike and basses. Those most susceptible to *Ichthyophthirius* were the suckers, dace and catfishes (Fig. 7).

As was to be expected, other parasites, which in an open system were insignificant, made their appearance in great numbers when the closed circulation was put into use. Most important among these were the gill and skin flukes (*Gyrodactyl-oides*). These parasites were never important, because in a fast flowing, open system, eggs and free-swimming larvae are usually washed to the sewer whereas in a closed system they remained to infect other fishes. There are probably several species of the gyrodactylid forms responsible for the mortalities but insofar as could be determined they seem to belong to the single genus *Urocleidus*. The most susceptible hosts were the members of the Centrarchidae such as the green sunfish (*Apomotis cyanellus*), blue-gilled sunfish (*Helioperca incisor*), warmouth sunfish (*Chaenobryttus gulosus*), rock bass (*Ambloplites rupestris*) and calico bass (*Pomoxis sparoides*).

Fortunately, fish killed by the copepod parasite *Argulus* were limited to the species *Lepisosteus osseus* (long-nosed gars). The bowfins (*Amia calva*) were heavily parasitized by these crustaceans but their resistance was so great that when they were subjected to the salt-water treatment, only one fish died.

In 1941, another parasitic crustacean (*Lernae* sp.) reached epidemic proportions. The infestation had its start on the common goldfish in 1940. In the spring of 1941 other varieties of goldfish were infested and in the early part of the summer the parasites had attacked and killed nine common eels (Fig. 10), and by late summer made their appearance on such fish as brook and common suckers, green sunfish, warmouth, rock bass and small mouth bass. For both types of crustacean parasites, lowering the temperature below their reproductive threshold is an important prophylactic procedure.

#### A. OTHER DISEASES OF TEMPERATE FRESH WATER FISHES.

##### 1. Bacterial.

In 1940, a short-lived epidemic of *Bacil-*

TABLE II.

## CAUSES OF DEATH OF TEMPERATE FRESH-WATER FISHES.

Parasitic and Infectious Diseases.		
DISEASES	1940	1941
Diseases of Skin and Gills		
1. Saprolegnia (Fungus)	37	8
2. <i>Bacillus columaris</i>	14	33
3. <i>Ichthyophthirius</i> (ciliate)	42	1
4. <i>Chilodon</i> (Ciliate)	4	—
5. <i>Cyclochaeta</i> (Ciliate)	6	9
6. <i>Costia</i> (Flagellate)	1	—
7. <i>Ichthyophthirius</i> & <i>Saprolegnia</i>	13	—
8. <i>Ichthyophthirius</i> & <i>Cyclochaeta</i>	10	—
9. Myxosporidia (Cnidosporidia)	5	1
10. <i>Ichthyophthirius</i> and Gyrodactylid	25	—
11. Gyrodactylids (Trematoda)	48	4
12. Argulus (Copepod)	48	1
13. <i>Lernae</i> sp. (Copepod)	9	33
14. <i>Lernae</i> and Gyrodactylid	—	4
Diseases of Skin and Internal Organs		
15. Lymphocystis	1	—
Diseases of Digestive System		
16. Enteritis due to Nematodes	1	—
17. Hepatitis due to Cestodes	—	1
Diseases of Circulatory System		
18. Pericarditis due to Neascus Infection (Trematoda)	1	—
19. Ruptured Sinus venosus (due to Gordiid worms)	—	1
Diseases of Internal Organs (General)		
20. Infectious Lymphosarcoma	8	4
21. Degeneration of Kidney, Liver, and Reproductive Organs due to Strigeid Worms	2	—
22. Degeneration of all Organs due to Gordiid Worms	—	5
Total	275	105

## Non-Infectious and Non-Parasitic Diseases.

DISEASES	1940	1941
Neoplastic Diseases		
23. Myxomata	1	—
24. Epithelioma	1	—
25. Osteoma	1	—
26. Ovarian tumor	—	2
Diseases of Digestive System		
27. Prolapsed Intestine with Stenosis	1	—
28. Liver Degeneration	5	1
29. Ruptured Gall Bladder	—	1
Diseases of Urinary System		
30. Kidney Degeneration	7	—
Diseases of Reproductive System		
31. Ovarian Degeneration	8	4
Diseases of Circulatory System		
32. Arterial Degeneration	—	5
33. Internal Hemorrhage	—	1
Diseases of Bone and Organs of Locomotion		
34. Lordosis	1	—
35. Atrophy of Tail Fin	2	—
Diseases Due to Nutrition		
36. Malnutrition	2	—
Senility		
37. Death Due to Old Age	5	—
Death Due to External Causes		
38. Temperature Changes	80	—
39. Causes unknown	41	—
Total Non-infectious Diseases	155	14
Total Infectious Diseases	275	105
Grand total	430	119

*lus columaris* occurred among the several species of catfishes (Fig. 6), the disease reappearing during the summer months of 1941. The bacilli were first described by Davis (1922) from a variety of fish hosts, including the catfishes. However, Davis had not determined any specific staining reaction for these organisms. In our studies, it was demonstrated that the bacilli are gram-negative in reaction. They are long, slender motile rods and within the measurement range given by Davis (5-12 x 25-.50 $\mu$ ). In the flat-headed catfish (*Ameiurus platycephalus*) and mud catfish (*Opladelus olivaris*), the disease was characterized by multiple circular patches scattered over the entire body, while the lesion in the common bull head (*Ameiurus nebulosus*) was characterized by a single circular growth on the dorsal part of the body, almost in the mid-line. These growths are grayish in appearance, rimmed by a well-defined hyperemia. Later the skin sloughs, exposing the under-

lying tissues. The lesion never penetrated beyond the skin. An interesting fact concerning this bacterial disease is that once the skin is sloughed, the disease is terminated. However, it reappears on another part of the body unless the fish is removed from the infective tank. Occasionally, a secondary infection with *Saprolegnia* may occur. If the lesions due to *B. columaris* are too extensive, death results. However, in many cases the disease was successfully treated by exposing infected fish to a 1:4000 solution of formalin. The treatment was effective only in the initial stages of the disease. A tank of fifty young bull heads so treated resulted in a complete cure with the loss of only five fish.

2. *Saprolegnia*.

This fungus attacks fresh-water fishes which have been injured either mechanically or by parasites. Handling thus represents a constant hazard, since spores of this fungus are omnipresent.



### 3. Lympho-sarcoma.

This neoplastic disease is classified here because of the infectious nature indicated. A number of northern pikes (*Esox estor*) from two to six years old began to die in January, 1940, with other deaths occurring periodically throughout the year. Autopsies revealed large, massive growths on the kidneys and abscesses in the livers. The tumors on the kidneys were, in some instances, grayish and granular in appearance, with practically the entire posterior part of the organ involved. Histologically, this structure presents a diffuse growth of lymphoid cells lying in reticular tissue. There was a certain amount of post-mortem degeneration involved but there could be no doubt that these lesions were lymphosarcomata. In other cases, the growths were nodular (Fig. 9) and also grayish in appearance, which histologically showed an adenoma reproducing renal tubules. The relationship between these two types of neoplasms in the pike, which in some cases were found on the same kidneys, is not known.

The abscesses on the liver (Fig. 8) of diseased pikes were made up of "lymphoid cells" of similar appearance to those found in granulated kidney tumors, indicating that perhaps metastases had occurred. Much of the liver tissue was involved and fish so affected had tremendously enlarged gall bladders filled with a light brown, watery bile. Further studies on this interesting disease are being made and will be published soon.

Piehn (1924) reported the presence of lymphosarcoma in goldfish and adenoma of kidney of pike.

### 4. Larval Trematodes.

These parasites are the metacercarial stage of a group of digenetic trematodes belonging to the family Strigeidae. The adults of these flukes are found in birds and mammals. Van Cleave and Mueller (1934) have shown that the metacercariae of this family are of three distinctive types recognized as *Diplostomulum*, *Tetracotyle* and *Neascus*. According to these authors, "Each type has a more or less definite location in the host. Thus *Diplostomulum* is usually . . . found in the eye . . . *Tetracotyle* is found encysted in the muscles, mesenteries, or pericardium of the host, and is surrounded by a rounded, usually thick, cyst. *Neascus* has an ovate, thin cyst, and is found on the viscera or mesenteries, in the skin, and frequently in the pericardium." The damage to the tissues produced by the more active worms (*Neascus*) may be considerable. If a vital organ (liver, kidney) is involved, death will occur. It is of interest to point out that in several cases a heavy infestation was found in the gonads

of blue-gill sunfish, producing parasitic castration. Several cases of strigeidiasis (probably *Tetracotyle*) involving the pericardium of sunfish (Fig. 11) were encountered. It is difficult to say whether pericarditis produced by these encysted worms was fatal even though no other infections or disease were determined at autopsy.

It should be known that these parasites present no problem in aquarium management. Fish obtain the infestation in their native waters and nothing can be done in treating the disease because of the location in the host. Occasionally, as in the case of an infestation of long duration, the host eventually lays down a resistant cyst to wall off the parasites. The cycle is completed only if the infested fish is eaten by a definitive host (bird or mammal).

### 5. The Gordiacea or "Hairworms."

In 1941 from April to July, the writer reported a number of cases of infestation with hairworms (*Chorodes*). These worms are nemathelminth forms belonging to the Class Nematomorpha. They are larval in character and have been recorded as parasites of insects, annelids, snails and occasionally in man and in fish. Their presence in fish (as in man) must be considered accidental, even though a total of 19 cases were encountered among tropical, semi-tropical and temperate fresh-water forms. Among the last mentioned group were the brook trout (*Salvelinus fontinalis*), rainbow trout (*Salmo irideus*) and Kentucky bass (*Micropterus punctulatus*). The infestations of the tropical fishes (*Limia domincensis*, *Poecilia vivipara*, *Platyepoecilus maculatus* and *Poecilibrycon* sp.) produced greater tissue damage and the fishes had their bellies distended with large amount of serous exudate. In all cases, two worms, sexually immature male and female, were found in the body cavity strongly coiled around each other. The organs of the hosts were greatly displaced and the parasites had set up considerable tissue reactions. In the case of the bass, the sinus venosus was penetrated by the worms, causing hemorrhages.

The source of this infestation was not established. The cycle is not completely understood. The worms become sexually mature while in the free-living state, laying eggs in water which hatch into free-swimming embryos possessing a proboscis and hooks at the anterior end. It is by means of these hooks that the organism bores its way into the body cavity of some aquatic insect (mayfly larva?) or other arthropod. It is not known whether it can bore its way into fish tissue, either through the intestinal tract or through the body wall. In the present instances, aquatic Oligochaeta are the suspected vectors.

### 6. Cnidosporidian Parasites.

These parasites, as a rule, are not important agents in causing death of aquarium fishes. However, because of the direct mode of infection, they present a continual threat. The five deaths recorded for 1940 were common suckers (*Catostomus commersonii*) and were due to heavy infestations of gill forms belonging to the family Myxosomatidae. The spores were enclosed in cysts found on the gill lamellae. They were oval in shape with two polar capsules and the sporoplasm without iodophilus vacuoles. Except for the location, the parasites resemble *Myxosoma bibullatum* Kudo (1934) reported from the skin of the same host.

Two cases of infection with the Myxobolidae, *Myxobolus conspicuus* Kudo, were found in the snout of the red horse sucker (*Moxostoma aureolum*). These parasites, however, were not the cause of death of the fish. It is reported here because of the interesting tumor associated with the infection. The disease appeared as a large, smooth growth, and stained sections revealed the presence of typical spores and pansporoblasts in various stages of development in the subdermal regions. Associated with this infection was a definite hyperplasia of the prickle cells of the epithelium. Prickle cell tumors are rare, even among human beings, and further studies are being made. Other interesting tumor-producing myxosporidians were reported by Nigrelli and Smith (1938, 1940) (see Fig 1).

### 7. Non-Infectious Diseases.

The percentage of deaths due to non-infectious diseases was considerably higher in 1939 than either in 1940 or 1941.

Several interesting cases of neoplasms are reported among which is a myxoma of the skin of rock bass (*Ambloplites rupestris*) (Fig. 13) and "lip" tumors on brook and rainbow trouts (*Salvelinus fontinalis* and *Salmo irideus*). The history of the disease in the rock bass is very interesting in that it may throw some light on the origin of the myxoma. Earlier in the year (1940) the fish was heavily infested with *Chilodon*, a protozoan ciliate, and the body covered with typical grayish mucus. The condition resolved itself and later a translucent, whitish patch remained. It has been observed many times that fishes heavily parasitized with external forms exude tremendous amounts of mucus. An examination of this material usually reveals many cellular elements, other than parasites, among which may be found some cells that exhibit amoeboid movements. In stained preparations the mucus contained stellate-shaped cells and eosinophiles, which are typical components of the myxoma under discussion. Among the 1939 mortalities, 13 cases of myxomata were reported.

The "lip" tumor of the brook trout is a hyperplastic growth of epithelial cells and, therefore, a true epithelioma. A similar case was reported in 1940. The "lip" tumor on the rainbow trout was an exostosis of the tip of the lower jaw bone. Both of these types of tumors are traumatic in origin, the result of the fish banging into the wall of the aquaria (see Fig. 17).

Incidences of prolapsed gut in fishes are not rare. Nigrelli and Breder (1935) reported an interesting case in the tropical fish *Mollienisia latipinna*, in which the prolapsed part of the intestine was completely everted and the lumen filled with cords of cells derived from the serosa. A somewhat similar condition was found in a rock bass (*Ambloplites rupestris*) (Fig. 12). This fish was a seven-year-old female and what brought on the eversion is not known. The bass was healthy in all other respects and was kept alive for several months, later being sacrificed for study.

The five cases of arterial degeneration reported in 1941 occurred in calico bass (*Pomoxis sparoides*) from three to five years old. Hemorrhages through the gills were noted in some of the specimens and while still in a moribund condition the fish were killed and autopsied. The blood vessels were firm and when handled with forceps were found to be friable. Just what is the cause of this "sclerema" is not known. It should be mentioned that so far, there is no evidence to show that fishes are subjected to the types of arteriosclerosis reported for mammals and other vertebrates.

The liver degenerations reported for fishes may be of several types. Most common disturbance is atrophic cirrhosis. In advanced cases very little of the liver pulp is present. Since no infection has been determined, it is assumed that the condition may be due to a deficiency of nutilites.

The kidney degeneration shows up as a complete breakdown of the organ. In many cases only small bits of kidney tissue remain, usually in the anterior region of the body cavity. Just how such fish carry on the excretory function is not known. There is some evidence in the literature that a certain amount of excretion may take place through the gills. As in the cases of hepatic degeneration, renal damage may be due to dietary deficiency and evidence from experimentation on other vertebrates indicates that they may be due to a deficiency in choline, one of the factors in the B-complex.

## IV. CAUSES OF DEATH OF FRESH-WATER TROPICAL FISHES.

(TABLE III).

The tropical forms include some of the smallest of fishes and it is difficult to perform adequate autopsy. These fish are kept



TABLE III.  
CAUSES OF DEATH OF TROPICAL FRESH-  
WATER FISHES.

Parasitic and Infectious Diseases.

DISEASES	1940	1941
Diseases of Skin and Gills		
1. Saprolegnia (Fungus)	1	—
2. Tuberculosis	—	3
3. Ichthyophthirius (Ciliate)	6	13
4. Gyrodactylids (Trematode)	5	2
5. Ichthyophthirius and Gyrodactylids	28	—
Diseases of Circulatory Organs		
6. Ruptured Sinus venosus (due to Gordiid Worms)	1	—
Diseases of Internal Organs (General)		
7. Mechanical Destruction of Internal Organs by Gordiid Worms	—	14
Total	41	32

Non-Parasitic and Non-Infectious Diseases.

Diseases of Digestive System		
8. Liver Degeneration	6	—
9. Biliary Cirrhosis	—	2
Diseases of Reproductive Organs		
10. Egg bound	—	1
11. Ovarian Degeneration	—	4

Diseases of Circulatory System

12. Ruptured Myocardium	1	—
13. Splenomegaly	1	—
14. Gas Embolism	—	1
15. Internal Hemorrhage	—	1

Diseases of Organ of Vision

16. Blindness	2	—
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Diseases of Bone and Organs of

Locomotion		
17. Swim Bladder Trouble	2	2
18. Lordosis	2	—

Unknown Causes

19. Edema (see Fig. 14)	3	1
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Diseases Due to Nutrition

20. Malnutrition	11	4
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Senility

21. Death due to Old Age	20	2
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Violent and Accidental Deaths

22. Fighting	33	14
23. Jumped Tank	6	1

Death Due to External Causes

24. Temperature changes	2	12
25. Changes in Water Chemistry	33	5
26. Unknown	73	38

Total Non-Infectious Diseases 195 89

Total Infectious Diseases 41 32

Grand total 236 121

in tanks with temperatures ranging from 70-80°F. and unless the fish is taken while still in a moribund condition or sacrificed when the disease first appears, it is difficult to make a proper diagnosis since post-mortem degeneration will often cloud the primary cause. It is for this reason that the highest percentage of mortalities are included in the category of causes unknown. This is shown in Table V. However, it will be noted that there was a great increase in infectious diseases for both 1940 and 1941. The agents for these deaths were limited as to kind, being typical of the forms one would expect to find among any fish collection. The ciliate, *Ichthyophthirius*, and the monogenetic fluke of the group *Gyrodactyloides*, are responsible for the greatest number of mortalities.

In 1940, three cases of tuberculosis were found in platyfish, *Platyepoecilus maculatus*. The disease was known to occur in this fish for some time but it was only recently described in detail by Baker and Hagan (1942). The organism has been identified as a specific agent, *Mycobacterium platypoecilus* and differs from all other strains of known acid-fast bacteria, except one which lives as a saprophyte in the soil. These investigators were able to culture the organisms on glycerol phosphate agar at room temperature and at 37°C. They also were able to reproduce the disease in normal platys and goldfish with the cultured material.

In 1942, an epidemic of tuberculosis broke out among other tropical fishes which included the following forms: neon tetra (*Hyphessobrycon innesi*), white cloud mountain fish (*Tanichthys albanuchus*), pearl danio (*Brachydanio albolineatus*), spotted danio (*Brachydanio analipunctatus*), and zebra danio (*Brachydanio rerio*). The lesions found on these fishes were typical, externally appearing as whitish patches on the dorsal side of the body. The growths were first seen on the head and gradually spread over the entire skin. Stained smears from skin lesions demonstrated large encapsulated rods usually found in cells identified as macrophages (Fig. 15). However, the organisms varied considerably in form and size, and in staining reaction. Some were minute, almost round in shape, while others were long and slender. The longer rods were only faintly colored with acid fuchsin. Histological examination of all the internal organs indicated the presence of these pathogens, particularly in the kidney, spleen and liver. The lesions produced were more pronounced in the kidneys, where much of the tissue was involved.

Whether the acid fast organisms found in these fish are the same as those found in the platy was not determined. Attempts to culture them have so far been unsuccessful but further studies are being conducted to determine this point and also their origin.

As was mentioned previously, water conditioning is a prime factor in maintaining

these small, fresh-water tropical fishes. In both 1940 and 1941, 14% of the deaths were attributed to conditioning disturbances.

#### V. SUMMARY OF THE FACTORS CONTRIBUTING TO MAJOR LOSSES OF FISHES IN CAPTIVITY.

As may be seen from Tables I-III, the causes of diseases and death of fishes in captivity are numerous and by no means limited to infections by animal or by plant parasites. Epidemiological studies among aquatic vertebrates have revealed that the factors involved are about the same as one would expect for human populations or for any other group of animals. The following are some of the more important physical, chemical and other factors to consider in preventing major catastrophies of fishes kept in captivity.

##### 1. CROWDING.

Breder and Coates (1931) have established the fact that there is a definite population density of fishes for a given volume of water. They showed that when the ratio of volume of fish to volume of water (surface area remaining constant) exceeds the optimum density, fish will kill each other off to maintain the population at equilibrium, when all other ecological factors are equal.

Any increase in numbers of fish (total volume of fish remaining the same) offers more body surface which may be attacked by parasitic agents. Ordinarily, there may be a few parasites present on the body, which under conditions of crowding will increase in numbers to the extent that the minor effects of the individual parasite is multiplied many times and the vitality sapped exceeds the margin of safety. As an immediate result of crowding, the mortality of the host species increases greatly and the epidemic rages until the contaminated tanks are depleted or an immunity is developed by the host.

##### 2. TEMPERATURE.

Fishes, particularly those of the temperate fresh-water variety, can withstand a comparatively wide range of temperature, but only if the changes are gradual. For certain psychrophilic and thermophilic types, the temperature range tolerated, even though the change may be gradual, is much restricted. In all groups of fishes, sudden change of temperature, even of a temporary nature, is a great shock to the fish and often fatal.

Fishes subjected to sudden temperature changes, small or large, very often become susceptible to infestation by one or more of the parasitic ciliates (*Ichthyophthirius*, *Chilodon*, *Trichodina*, etc.). The rapidity

with which these parasites appear on the skin of fishes after such a change is as yet not thoroughly understood. In the case of *Ichthyophthirius*, the writer believes that a drop in temperature induces encystment. It is in the encysted stage that the ciliate undergoes multiplication, each individual cyst capable of producing hundreds of infective organisms. MacClennan (1937) showed that the transformation of ciliophores which are unable to encyst or divide to mature stages which can encyst and produce infective individuals is a very rapid one. Increasing the temperature induces excystment, resulting in the liberation of the young ciliophores. These young forms are very susceptible to changes in osmotic pressure so that adding salt-water to make up a solution of one-half strength (sp. gr. about 1.0150), or sodium chloride to make up a solution of .5%, will kill these organisms (and other ectoparasitic protozoa or flukes) with little or no effects to the host.

Since it is known that reproduction among organisms is definitely correlated with temperature, the ability to control this factor at any definite point becomes an important prophylactic measure in aquarium management.

##### 3. LIGHT.

That an optimum amount of light is an essential requirement to maintain fishes in good health is quite evident. Breder and Harris (1935) have analyzed the effect of light on orientation and stability of certain fish species, particularly young filefish and young cowfish. If such fish are exposed to a beam of light, they lose all sense of orientation and move about in rapid gyrations. As to the harmful effects of strong light, they state, "In fact it seems to be definitely established that violent or continuous changes in orientation of fish is decidedly harmful, if not indeed fatal to the fish."

The relationship of light disease-producing agents is not definitely known. There is much evidence in the literature concerning the phototropic reaction of parasites. Increasing the amount of available light over the fresh-water tanks was followed by an epidemic of lernaiasis and may be partly attributed to this factor, especially in the movements of the larvae of these fixed parasites. It is a known fact that larval trematodes are positive-phototropic and may account for the predominance of monogenetic forms on surface fishes.

##### 4. H-ION CONCENTRATION.

The range of the degree of acidity or alkalinity (pH) that fishes can tolerate varies considerably with the species. The optimum pH value for marine forms is around 8, while the optimum for fresh-water species is around the neutral point

(pH 7.0). As will be shown, fishes can and do control, to a certain degree, the chemical contents of their environment. That they play some part in adjusting the pH of their environment can be shown by taking a pH reading of water before and after fishes have been included. Comparatively few species of fishes are favored by completely acid water (i.e., below pH 7); most of them live in water on the alkaline side of the pH range.

The chemical control of sea water for aquaria has been thoroughly established by Breder and Howley (1931) and the technique perfected by these investigators is now in use in most aquaria. They point out the necessity of a careful check on the bicarbonate salts. These are buffering agents needed to maintain the reaction at a proper level but which are continually broken down by the acid metabolites of aquatic organisms.

### 5. Specific Gravity.

The optimum density of sea-water for the proper maintenance of marine animals is established by the density under natural conditions. The harmful effects on the tissues of fishes of changes in density and salinity of water has been studied by Sumner (1906) and more recently by Keys (1931). The latter worker has shown that an increase in density raises the respiratory rate, hence increases metabolic activity. Many species can tolerate abrupt changes in density, and while prolonged exposure to high or low densities do produce deleterious effects, the degree of damage may vary considerably with the species. This is accounted for, in part, by the fact that in the former case the body tissues have had no time to make adjustments for the differences in osmotic pressure, and nothing is lost or taken in. Invertebrates, however, cannot tolerate even comparatively slight changes in density and salinity and for this reason are extremely difficult to keep under aquarium conditions for any length of time.

Since fishes have a greater tolerance than parasites (invertebrates) for changes in the tonicity of their environments, the control of the specific gravity also becomes an important prophylactic and therapeutic measure.

### 6. Flow and Aeration of Water.

Some fish require fast moving bodies of water with a high oxygen content. Any depletion in the oxygen threshold for fishes of high metabolic activity may be fatal. Methods of controlling the oxygen supply or the reduction of tension of other and more harmful gases are many. Artificial aeration, green plants, increasing the surface area, increasing the flow, lowering the temperature, etc., are all aids in keeping the

oxygen tension at optimum level. Too much oxygen may be just as detrimental as too little of this important gas. It is a known fact that fishes may develop gas embolisms, producing hemorrhages in various parts of the body, especially of the surface capillaries. Chlorine and nitrogen are other gases which may be present in water and which can be toxic in certain concentrations.

### 7. Metabolic Waste Products.

It is known among Ecologists that fishes living in small standing bodies of water alter the chemical content of their environment, apparently not only making it more suitable for themselves, but sometimes rendering it completely toxic for even closely related species. This has been called water conditioning. It is a very important factor in maintenance of fish in captivity, especially the small fresh-water tropical varieties. Just what this conditioning is, has so far evaded successful analysis. Evidence indicates that some specific animal protein or protein derivatives may be involved. Among marine species it is known that a tank of elasmobranchs will produce a sufficient concentration of metabolic waste materials to be toxic for many teleost species when placed in it.

### 8. Diet

Many diseases of fishes kept in captivity are due to vitamin deficiencies. Raw fish, both frozen and fresh, forms an important item in the diet of fishes kept in captivity. Fishes placed entirely on such a diet will show certain definite symptoms, such as loss of appetite, excitability, loss of coordinated movements, etc. According to Wolf (1942), similar symptoms developed in trout under experimental conditions were alleviated by the addition of vitamin B<sub>1</sub> to the diet.

As was mentioned above, the large number of liver and renal damages encountered during autopsies may lead to an inference of a deficiency of certain other essential nutrilites. Since it has been determined that choline is indicated for similar conditions in higher vertebrates, experiments are now under way to determine the efficacy of this compound for these diseases in fish.

### 9. Handling and Permanency of Location.

Handling is a very important item and directly or indirectly may be responsible for the deaths of large numbers of fishes. Fish handled will invariably receive abrasions which become the focal point of infection with bacteria or molds. If the injured surface area is large, death will result.

Fishes collected during the spawning season are a poor risk as exhibition speci-

TABLE IV.

COMPARISON BY MONTH OF THE NUMBER OF DEATHS OF FISHES FOR 1939, 1940 AND 1941 (8 MONTHS ONLY).

	1939			1940			1941		
	M	T	Tr*	M	T	Tr	M	T	Tr
Jan.	25	0	21	34	18	19	33	10	10
Feb.	43	6	15	34	27	23	24	7	18
Mar.	40	0	34	20	16	13	26	6	18
Apr.	47	2	24	30	33	36	26	13	21
May	67	14	43	84	7	19	29	6	10
June	78	7	16	63	120	14	27	13	9
July	328	34	45	63	126	22	17	43	17
Aug.	115	7	18	46	26	31	13	21	18
Sept.	62	6	21	35	18	16			
Oct.	52	9	12	35	16	23			
Nov.	38	54	15	23	4	13			
Dec.	32	71	12	26	19	8			
Total	927	210	276	493	430	236	195	119	121

\* M, Marine; T, Temperate Fresh-water; Tr, Tropical Fresh-water.

TABLE V.

SUMMARY OF MORTALITY PERCENTAGE BY CAUSES.

CAUSES	1939	1940	1941	1939	1940	1941	1939	1940	1941
Infectious	68.00	40.80	37.00	60.50	64.00	88.20	13.90	17.00	26.50
Non-Infectious	13.00	20.50	25.00	20.50	7.90	11.80	31.10	21.00	15.00
Violent Deaths	4.00	7.90	18.00	.50	00.00	00.00	1.10	17.00	12.40
Water Conditions*	11.00	17.20	2.00	13.30	18.60	00.00	31.10	14.00	14.10
Unknown	4.00	13.60	18.00	5.20	9.50	00.00	32.80	31.00	32.00

\* Includes density, Temp., pH and Chemical Composition.

mens. They do not successfully withstand rough handling and long truck or boat trips. Many fresh-water species spawn in the spring, on the rise in temperature. Such fish have not recovered from the winter's starvation, and are usually heavily parasitized. Fish that spawn in the fall, i. e., on the drop in temperature, are a better risk, for they have had an opportunity to build themselves up and therefore can withstand the rigors of capture more successfully. Because of the temperature factor, cold water forms should not be collected during the summer months unless proper refrigeration facilities are available.

Once a fish or group of fishes become established in a tank, removing them to other sites results in a high incidence of deaths. In spite of the fact that the water is the same (homotypic) in their new tanks, the fishes become highly nervous, dash about and bang their snouts against the walls. They finally settle to the bottom, refuse all food and eventually die.

Another interesting reaction to permanency of location is the behavior of long-established inmates of a particular tank to new members introduced, even of the same species. The new fish, regardless of size, are often attacked and severely injured or even killed by the established fish or fishes.

## 10. Parasitism.

All fishes should be examined for parasites, especially external forms. The importance of this procedure is obvious and has been reported by Nigrelli and Atz (1943). It should be pointed out further that under epidemic conditions, many of the external parasites show no host specificity and the virulence is increased many fold.

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## EXPLANATION OF THE PLATES.

(All pictures by S. C. Dunton, Photographer N. Y. Zool. Soc.)

## SOME DISEASES OF MARINE FISHES.

## PLATE I.

- Fig. 1. *Cyprinodon variegatus* with myxosporidian (*Myxobolus lintoni*) tumors. 3  $\times$ .
- Fig. 2. *Epibdella melleni*. Round pompano (*Trachinotus falcatus*) heavily parasitized with this monogenetic trematode. About 2  $\times$ .

## PLATE II.

- Fig. 3. *Echinorhynchus proteus* (Acanthocephala). Intestine of striped bass (*Roccus lineatus*) showing a heavy infestation with these spiny-headed worms. Note perforations of the intestinal wall and thickened mucosa. About 2  $\times$ .
- Fig. 4. Gas embolism. Brain of common jack (*Caranx hippos*) with hemorrhagic infarct. About 2  $\times$ .
- Fig. 5. Thyroid adenoma. Head of blue angelfish (*Angelichthys isabelita*) with thyroid tumor invading the gills. About  $\frac{1}{2}$  natural size.

## SOME DISEASES OF TEMPERATE FRESH-WATER FISHES.

## PLATE III.

- Fig. 6. *Bacillus columaris*. Mud catfish (*Opladelus olivaris*) showing typical dermatitis due to this bacillus. About  $\frac{1}{3}$  natural size.
- Fig. 7. *Ichthyophthirius multifiliis*. Channel catfish (*Ictalurus furcatus*) showing typical pustules on the skin. These are the encysted ciliates (Holotricha) which in time will burst open, each cyst releasing about 200 minute ciliophores. About 3  $\times$ .

## PLATE IV.

- Fig. 8. Infectious lympho-sarcoma. These liver abscesses in the pike (*Esox estor*) are associated with large granular masses involving the greater bulk of the kidney. Histologically, the cellular elements in both of these growths are mainly round cells. The infectious nature is indicated by the fact that several pikes of different ages autopsied at about the same time were found affected by this disease. Note enlarged gall bladder. About  $\frac{2}{3}$  natural size.
- Fig. 9. Kidney adenoma. Large nodular tumor in kidney of pike which histologically showed reproducing renal tubules. About  $\frac{2}{3}$  natural size.

Fig. 10. *Lernae* sp. Head of eel (*Anguilla rostrata*) split open to show the heavy infestation of this crustacean parasite (Copepoda). The parasites were mainly localized in the mouth cavity. About natural size.

Fig. 11. Strigeid flukes. Larval trematodes (Tetracotyle) encysted in the pericardium of common sunfish (*Lepomis gibbosus*). About 3  $\times$ .

## PLATE V.

- Fig. 12. Prolapsed gut. The protruding intestine shown in this rock bass (*Ambloplites rupestris*) is completely occluded by cellular elements derived from the serosa. About  $\frac{1}{2}$  natural size.
- Fig. 13. Myxoma. A mucoid growth on a rock bass which histologically shows the presence of typical cellular elements (stellate shaped cells and eosinophiles) usually found in these tumors. About  $\frac{1}{2}$  natural size.

## SOME DISEASES OF TROPICAL FRESH-WATER FISHES.

Fig. 14. Lymphocystis. This disease is characterized by a hypertrophy (increase in size) of connective tissue cells. The nodular growths shown in this striped sleeper (*Dormitator maculatus*) are made up of groups of these giant cells. 2  $\times$ .

## PLATE VI.

- Fig. 15. *Mycobacterium* sp. (*M. platypoecilus*?) from skin of Neon tetra. Note bacilli in large macrophage cells. 1800  $\times$ .
- Fig. 16. Edema. This disease is of common occurrence in many of the smaller tropical fresh-water fishes. The exact nature or cause of the disease is not known. In some, it is characterized by the presence of large amounts of serous exudate in the body cavity. In others, for example, the blind cave characin (*Anoptichthys jordani*), the material found in the body cavity is a translucent gelatinous-like substance of unknown nature. About natural size.
- Fig. 17. Lip tumor. Many fish in captivity develop lip tumors as a result of banging continuously into the walls of the tank. These tumors, like the one shown here in *Acestrorhynchus microlepis*, may be either osteomata or epitheliomata in character. About 3  $\times$ .



FIG. 1.

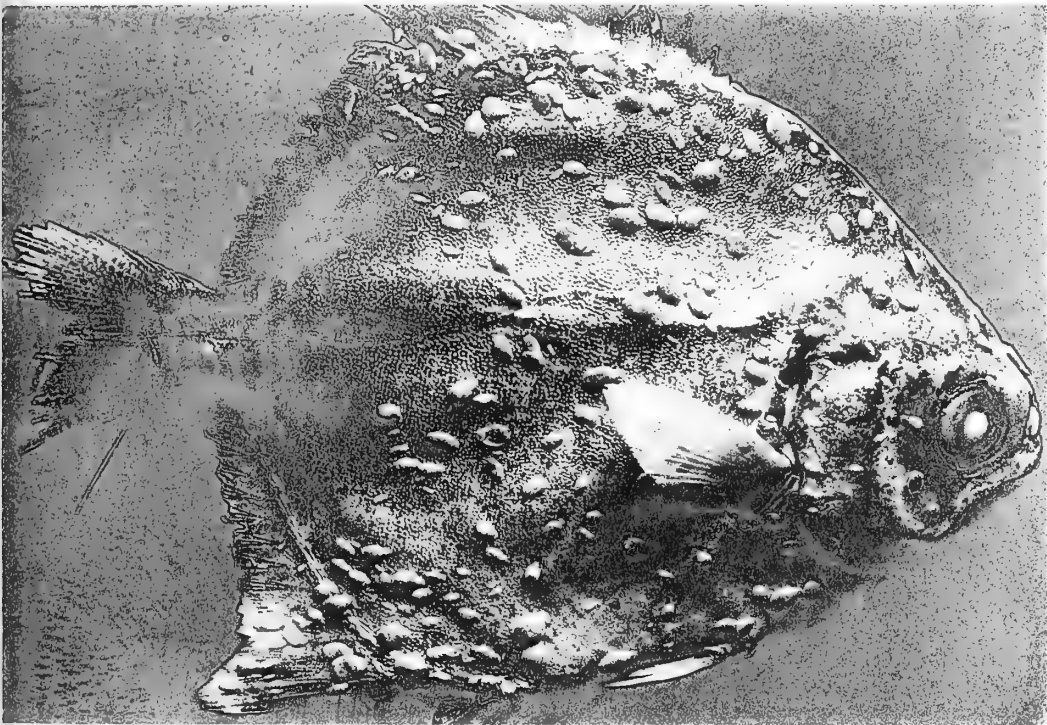


FIG. 2.

CAUSES OF DISEASES AND DEATH OF FISHES IN CAPTIVITY.





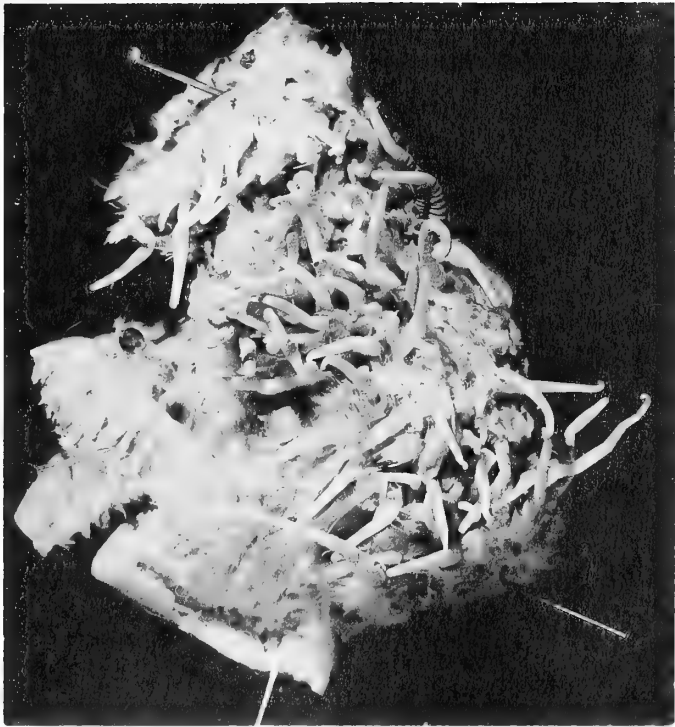


FIG. 3.



FIG. 4.



FIG. 5.

CAUSES OF DISEASES AND DEATH OF FISHES IN CAPTIVITY.



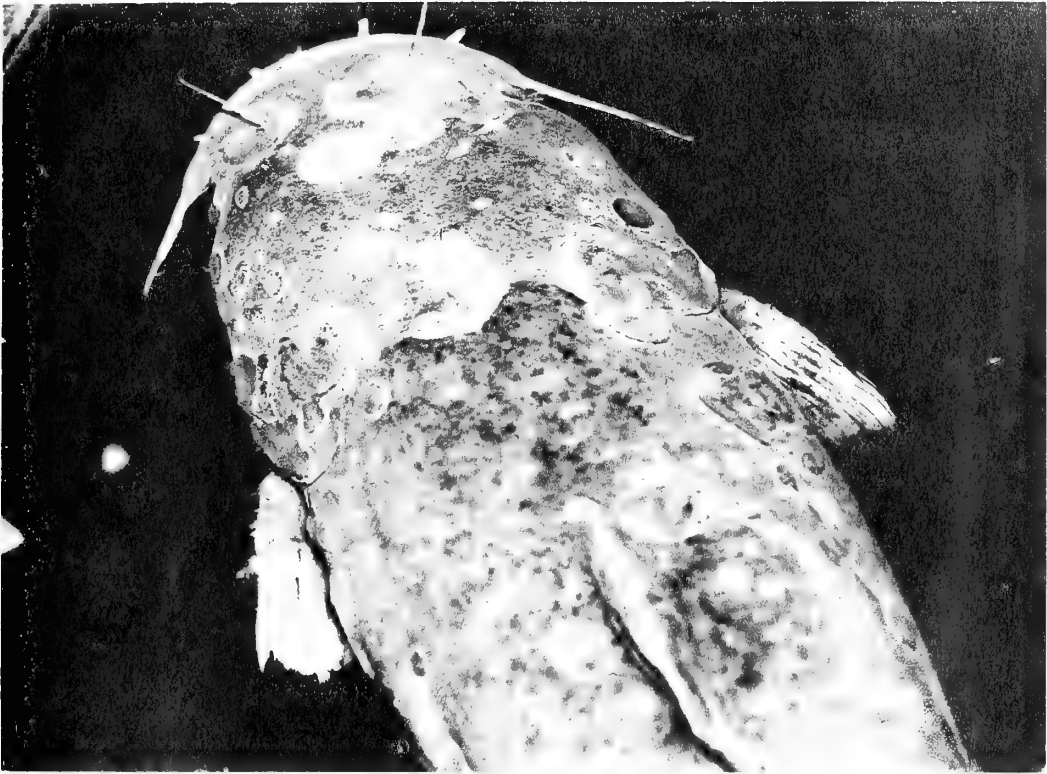


FIG. 6.

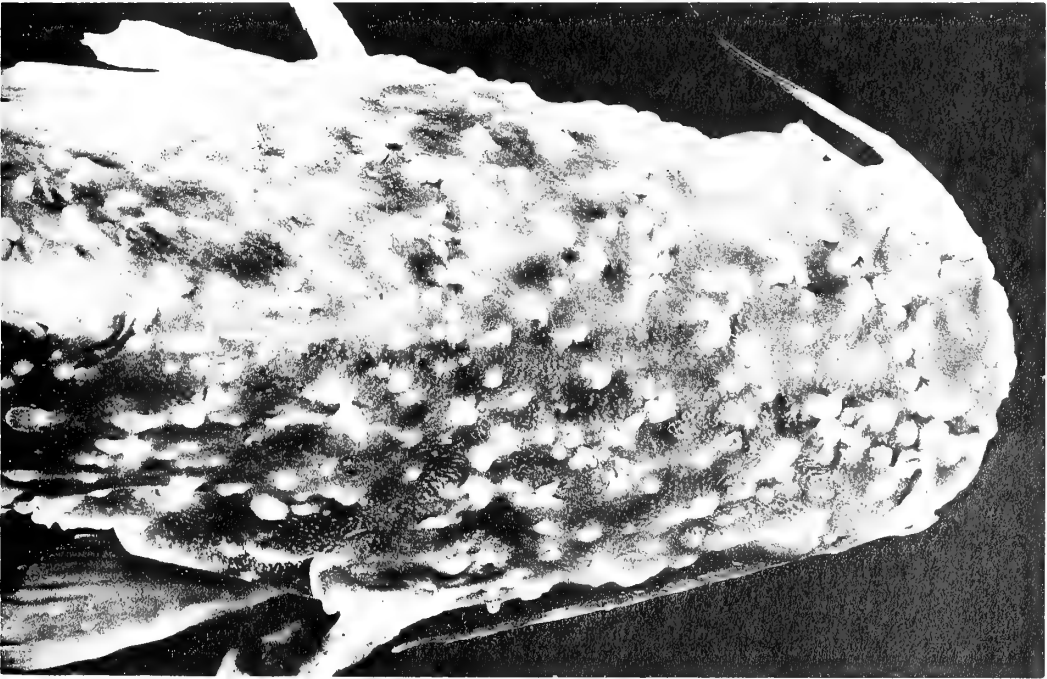


FIG. 7.

CAUSES OF DISEASES AND DEATH OF FISHES IN CAPTIVITY.



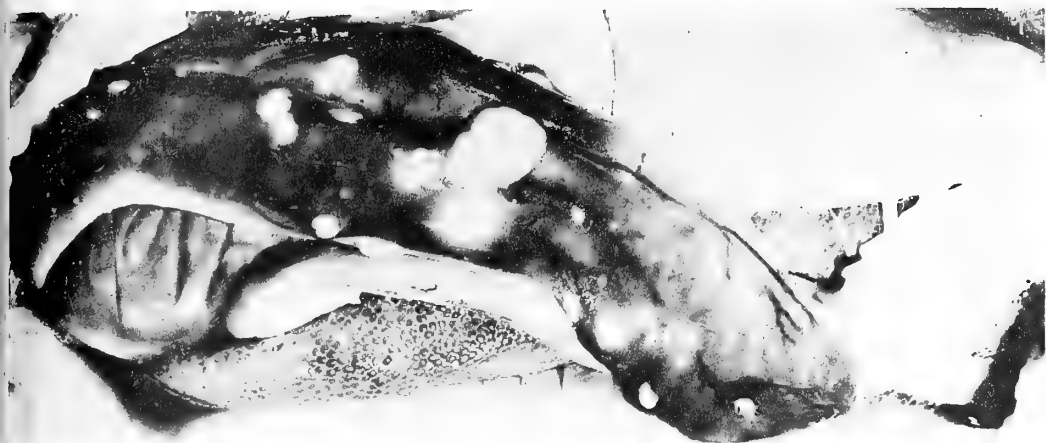


FIG. 8.



FIG. 9.



FIG. 10.

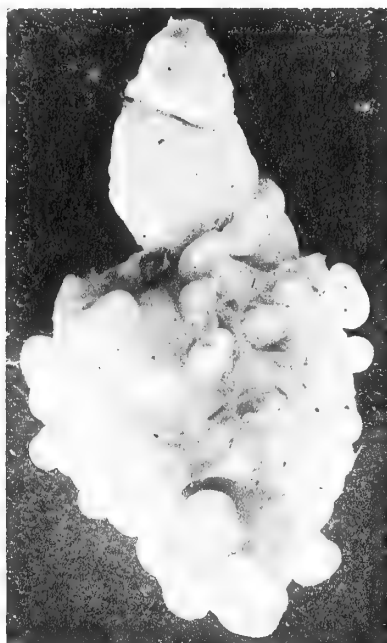
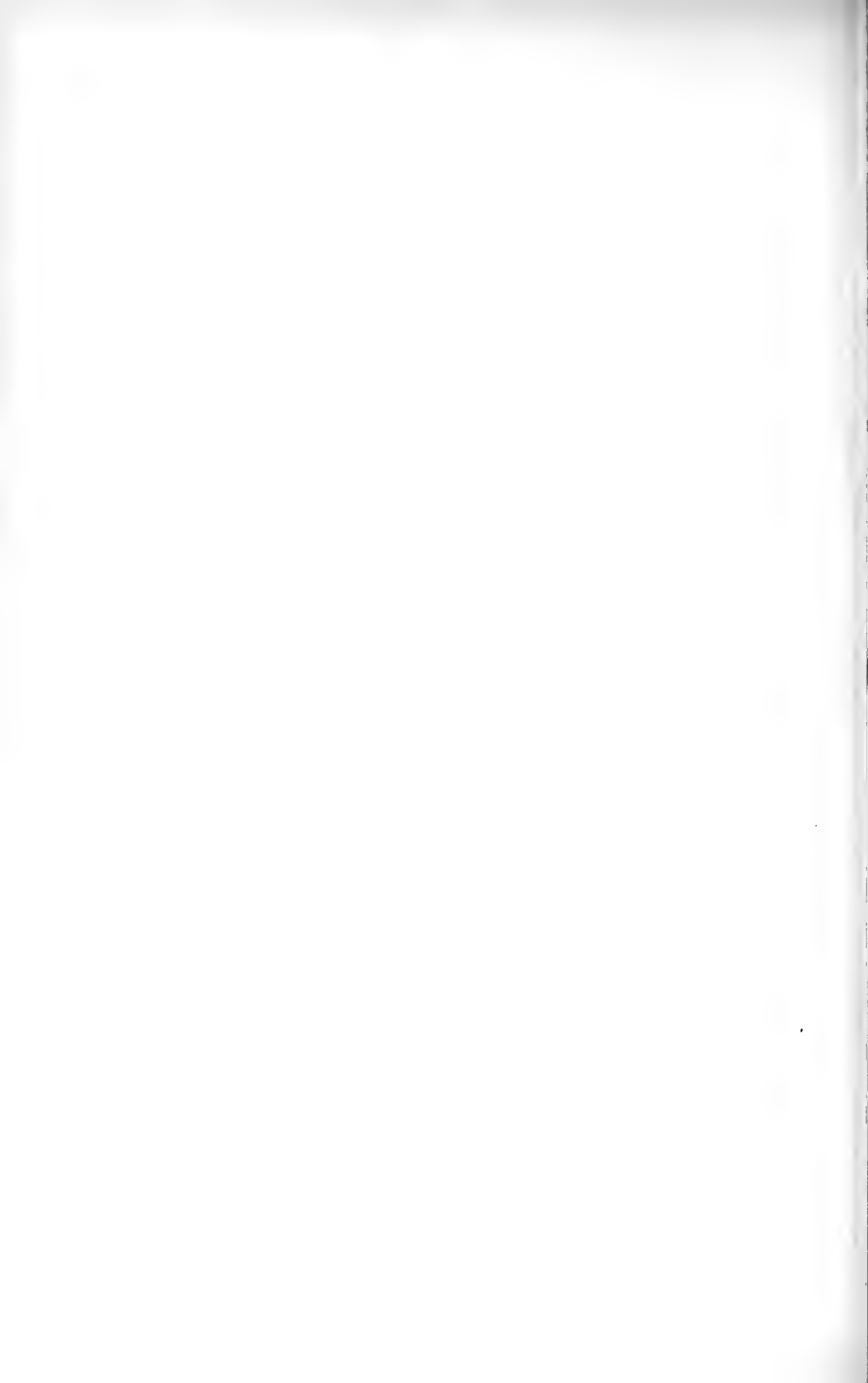


FIG. 11.

CAUSES OF DISEASES AND DEATH OF FISHES IN CAPTIVITY.



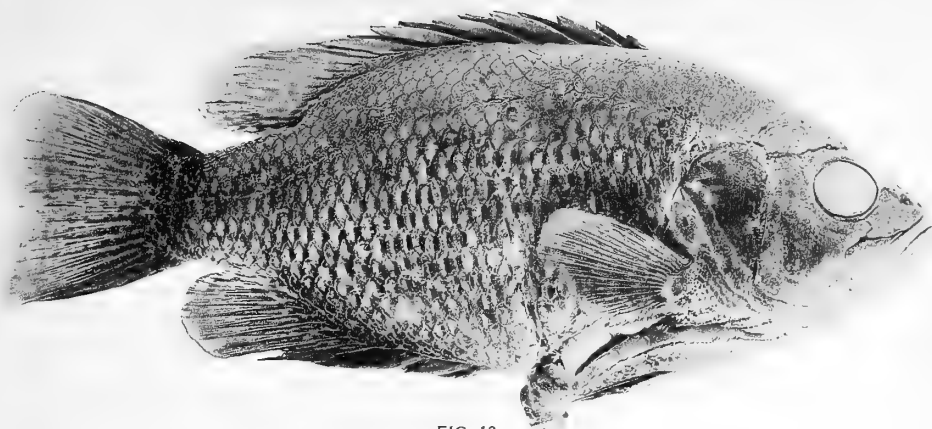


FIG. 12.

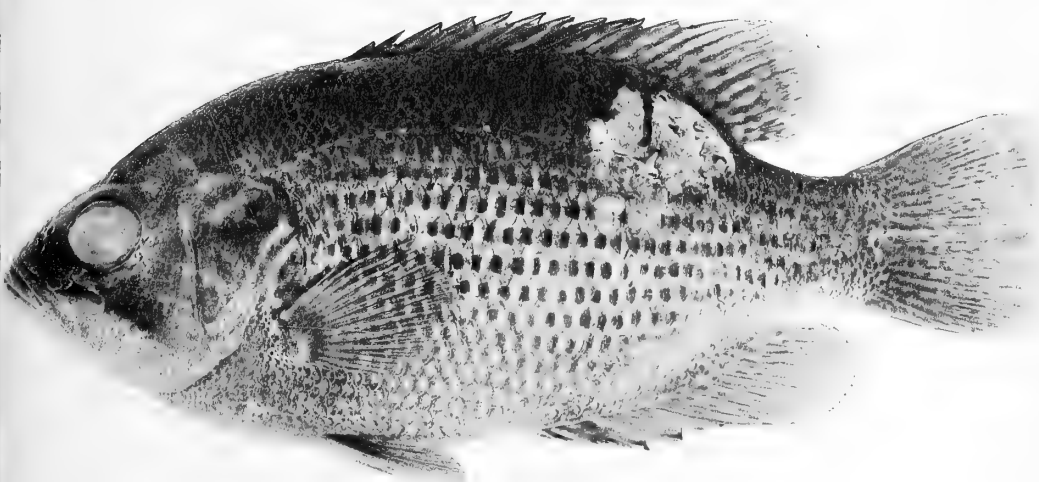
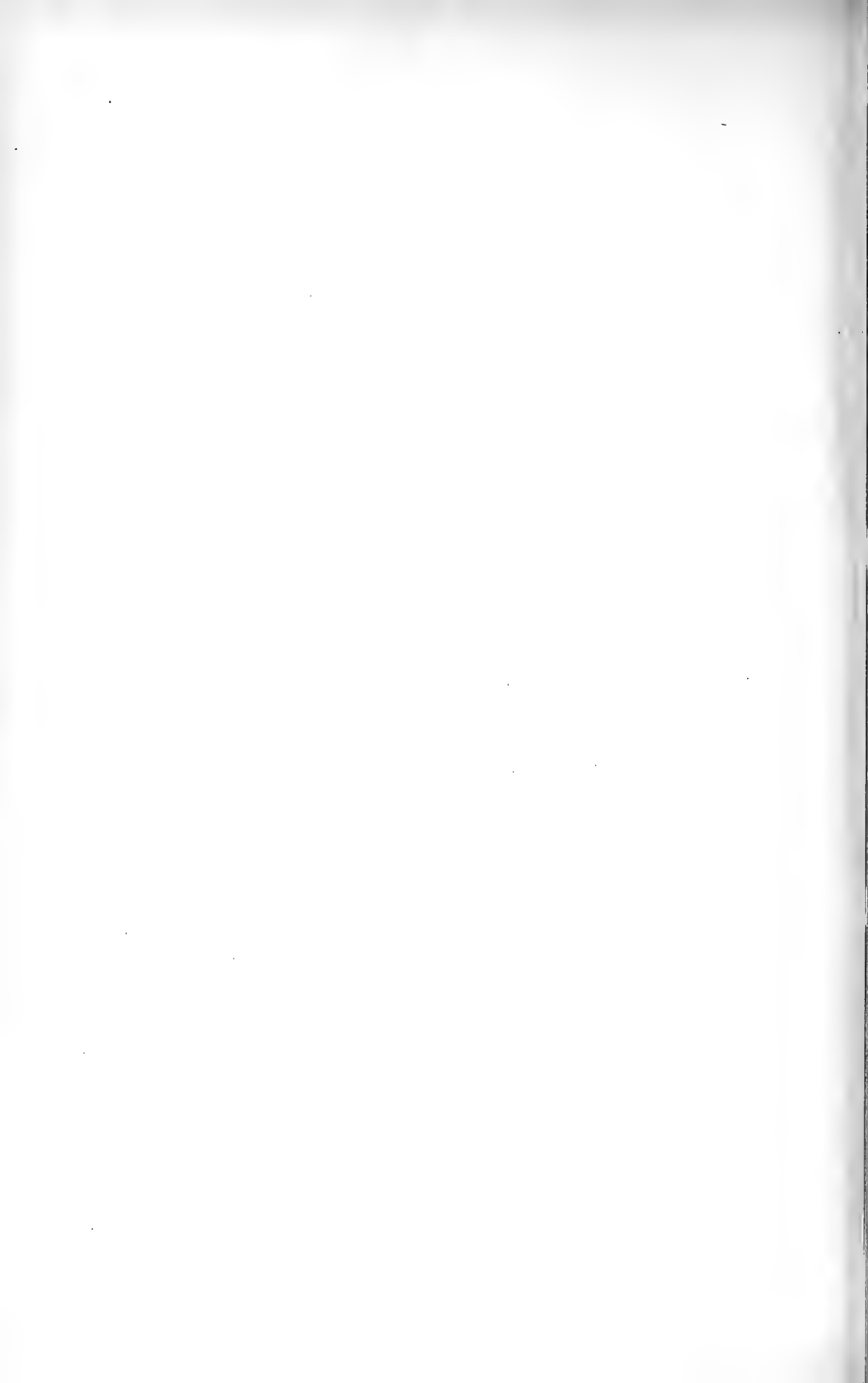


FIG. 13.



FIG. 14.

CAUSES OF DISEASES AND DEATH OF FISHES IN CAPTIVITY.





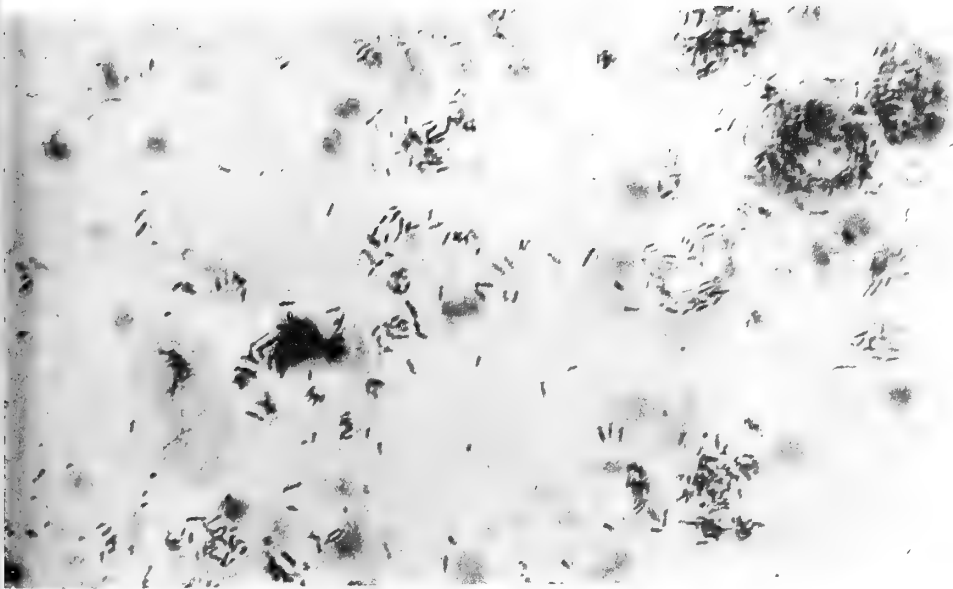


FIG. 15.

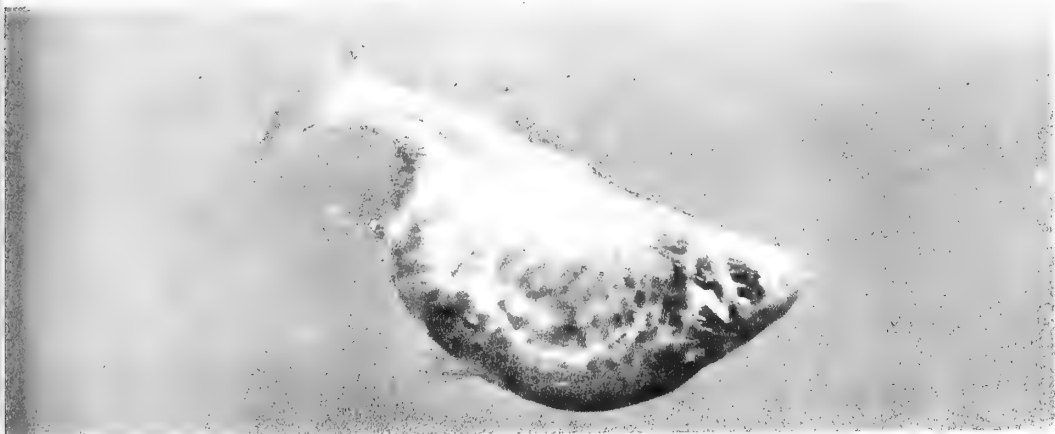


FIG. 16.

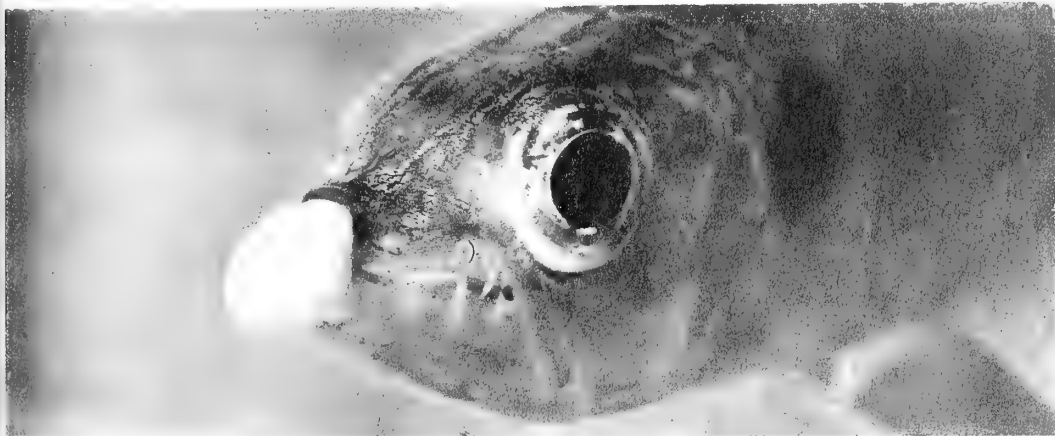
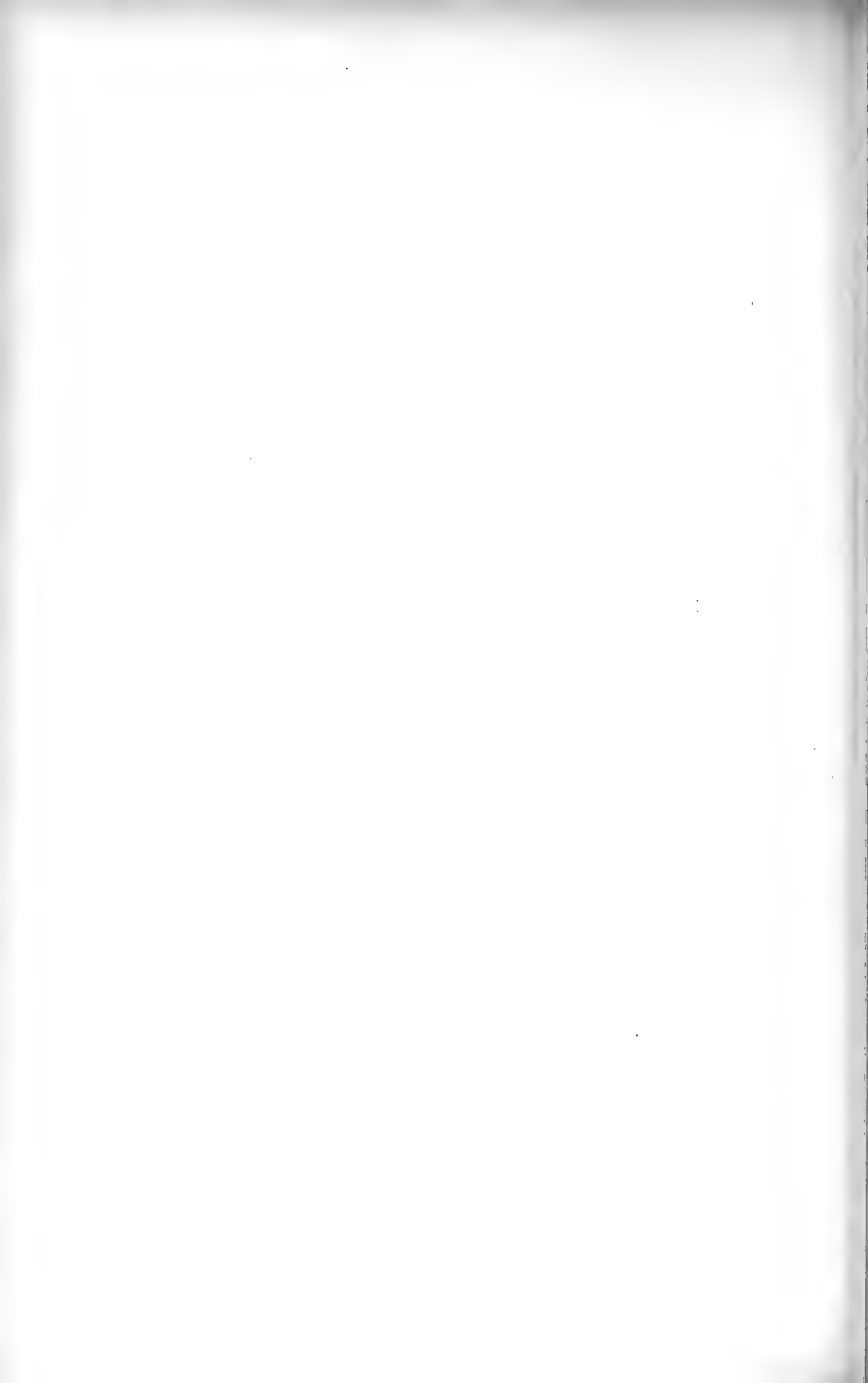


FIG. 17.



## 23.

Display, Breeding and Relationships of Fiddler Crabs (*Brachyura*, Genus *Uca*) in the Northeastern United States.<sup>1</sup>

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(Text-figure 1).

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## INTRODUCTION.

During the spring and summer of 1943, observations were made near New York City on the display and breeding season of two fiddler crabs, *Uca pugnax* and *U. pugilator*. A few similar notes were taken on the third local fiddler, *U. minax*, during 1941. The purpose of the study was to determine whether these northern fiddler crabs have specifically distinct displays such as were found (Crane, 1941, 1943) to be characteristic of tropical American species during the breeding season, and to see if these displays shed light on the phylogeny of the group.

Previous observers, especially Pearse (1914), Swartz and Safr (1915) and Gray (1942) in their excellent papers all observed waving in these northern species, but none reported any difference in the procedure of the several species. Pearse alone thought waving to be definitely concerned in courtship, at least to the extent of attracting the attention of the female, and not only as a defense of territory and as a threat to other males. But even Pearse concluded, after remarking that *pugnax* prefers muddy, *pugilator* sandy, locations, "Aside from these differences in habitat and the fact that *U. pugnax* bred earlier in the season than *U. pugilator*, no difference was noticed in the behavior of the two species."

That differences do exist became clearly evident to me during the past summer,

thanks entirely to previous experience in the tropics. Many of the southern species, studied on expeditions of the Department of Tropical Research under the direction of Dr. William Beebe, are more strikingly distinct in their displays than the northern forms, and so, logically, it was they which gave the key to display characteristics. Nevertheless, once the principle of specific behavior variation was understood, the differences between the displays of northern species were obvious at first glance. Finally, prolonged watching proved that without question, waving is an integral part of courtship, just as in tropical fiddlers.

In the present paper, displays and colors will be described in detail under specific headings, along with supplementary taxonomic characters, in order to make the work comparable with the tropical American *Uca* reports. General remarks on breeding season, display and unsolved problems are placed in the concluding section. The usual methods of study were employed: that is, the same beach or mud-flat was used as an observation post as often as possible, and binoculars were found to be invaluable.

The localities visited included Greenwich, Connecticut; Pelham Bay Park, Port Jefferson and Staten Island, New York; and Atlantic City and Quinton, New Jersey. My appreciation goes to Dr. and Mrs. Robert Cushman Murphy and to Mr. George Agnew Chamberlain for their hospitality during the study of these crabs.

*Uca pugnax* (Smith, 1870).

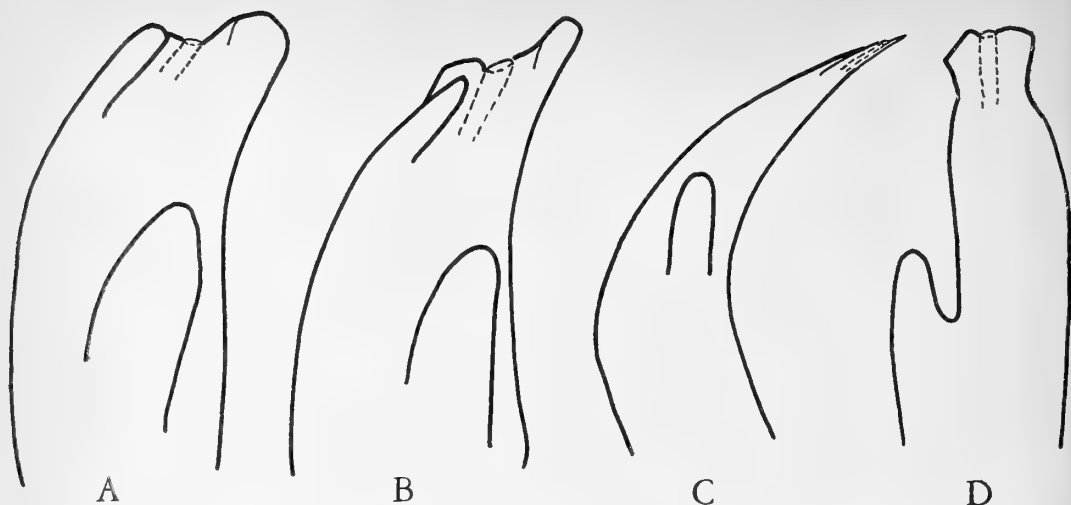
(Text-fig. 1a)

References: *Gelasimus pugnax* Smith, 1870, p. 131; pl. 2, fig. 1.

*Uca pugnax*, Rathbun, 1918, p. 395; pl. 139.

Range: From Cape Cod, Massachusetts, to Louisiana.

<sup>1</sup> Contribution No. 672, Department of Tropical Research, New York Zoological Society.



TEXT-FIG. 1. Tips of right abdominal appendages of adult males in *Uca*. **A**, *pugnax pugnax*, anterior view; **B**, *minax*, anterior view; **C**, *pugilator*, anterior view; **D**, same, lateral view. Hairs omitted.

**Supplementary Specific Characters:** A typical Group 2<sup>2</sup> *Uca*, in supplementary characters like *pugnax rapax* (Crane, 1943, p. 40), except as follows: there are fewer spoon-tipped hairs on merus of second maxilliped, usually between 10 and 20, rarely up to 25, instead of usually between 70 and 120, rarely as few as 25. Even the tips of the abdominal appendages are practically indistinguishable from those of the subspecies; female always with a well developed genital tubercle.

**Color:** Displaying males: Carapace dark brown, sometimes grayish or whitish at least on branchial regions in large specimens. Major cheliped outside and in dull brown or brownish-yellow, rarely (outside only) dull apricot yellow, with fingers or entire manus and chelae cream; manus sometimes creamy yellow; eyestalks, top of third maxillipeds and/or front bright turquoise blue (previously unrecorded); minor manus and chelae creamy yellow, sometimes greenish yellow, or even blue-green, almost as bright as the eyestalks. In this species there is relatively very slight brightening of color before display, compared with many tropical forms, or even with *pugilator*. Females scarcely or not at all mottled, dark, with chelae and mani like those of males.

**Display:** The display of *pugnax*, although obviously related to that of the southern *pugnax rapax*, differs from the latter to a much greater degree than would be suggested by the purely structural differences between the subspecies. Both are slow, as compared with more marine forms, but whereas strong jerking is marked in *pugnax*

*rapax*, it is indicated only very slightly in *pugnax*, while, on the other hand, a characteristic bobbing curtsy often begins or ends a *pugnax* display, which is never found in the southern form. Also, the display is more variable and sporadic than in *pugnax rapax*. Details are as follows:

The display starts with body elevated only moderately high, both chelae held well off ground and flexed in front of mouth. Major cheliped is unflexed obliquely upward with scarcely the faintest trace of jerking which might be unnoticeable except in view of knowledge of related forms in which jerking occurs. The minor is unflexed simultaneously. Usually with no pause at the peak, the major is brought down into position with something resembling a jerk, or more often several jerklets, as if let down in worn notches so that it slides down with the least hint of "braking." It is only in the most active displays that there is a hint of the pause at the top so characteristic of *pugnax rapax*. During display, as usual in the jerking Group 2 crabs, one or two ambulatories may be lifted and kicked outward at the peak of display. Several steps to one side are often taken on the down stroke. Chelae are usually held almost closed throughout, but sometimes open at the peak of display and sometimes are held open throughout.

At the beginning, or more often, at the end of a display, or sometimes without any waving whatever, a characteristic bobbing, or series of "curtsys" may occur, especially in crabs displaying directly to, or noticed by, a female. It does not precede fights between males, as far as I can see, any more

<sup>2</sup> For group characteristics, see Crane, 1941, p. 165.

than waving is speeded up before these encounters. This curtsy is not found in any of the other species which I have hitherto observed. It is so fast and slight a motion that it is difficult to analyze, but repeated observation shows the details to be as follows: the body is lowered, with both chelipeds flexed, and simultaneously a double, triple or quadruple tattoo is made with the ambulatories of both sides against the ground. Usually the two middle legs of each side seem to be the ones involved, and their action is frequently alternating.

A second specialization of display, even more climactic in character, was seen once, when the male had attracted a female's attention and had paused halfway down his hole for a final gesture. This took the form of a rigid extension of all the free appendages—major cheliped and four ambulatories—accompanied by a momentary strong vibration of them all. Exactly the same behavior was noted in *saltitanta* under similar conditions, except that in the latter species the cheliped was not involved (Crane, 1941, pp. 154, 191). In *pugnax*, the female did not follow, and the male soon reemerged.

It is impossible to time *pugnax* displays accurately, since they are so variable. However, the average, fast, complete display exclusive of curtsy lasts about 2 seconds.

**Rudimentary Shelter-building:** In *pugnax* there is evidence that the habit of shelter-building is present in its most elementary form. As in other builders, it occurs in some but not all individual adult, or nearly adult, males. Perhaps the ancestors of the species built always in banks, and the oblique angle of the burrows plus the plugging-up instinct combined to make a pushed-up archway over the door a natural result. This, however, does not explain its absence in the burrows of females. In a colony in relatively sandy soil, mixed with *pugilator*, at Port Jefferson, this habit was first noticed and was more striking than elsewhere: *pugnax* always chose the side of any surface irregularity, for the hole entrance, in preference to flat ground, and there was always in these cases a definite, overhanging hood, though small and poorly formed. This hood I have several times seen shored up with material brought from two or more inches away, just as in the case of true shelter-builders (e. g., *minax*, *cumulanta*, *beebi*, etc.). There is no trace of this behavior in *pugilator*, and the burrow entrances are always in flat areas.

**Posing:** In *pugnax* the usual brachyuran threat posture of standing motionless with both chelipeds spread wide was observed a number of times, but as Pearse noticed, it had, in this species, nothing apparent to do with fear or threat, either to rival males or

potential enemies. Females were seen to pose also, but not so often, and the majority of posers appeared to be immature. Often one or more ambulatories were kept elevated during posing; usually the crabs faced away from the sun, and remained out of their holes so long that they became quite light gray, apparently from dryness. Often a small elevation was chosen. Every little while they moved slightly, flexing chelae or shifting legs, but not changing ground. They seemed to a certain extent to go into a sort of trance, since they dodged and retreated less than the others when mildly disturbed—say, by a passing car—although when seriously startled, as by the observer's sudden motion, they reached their holes almost as quickly as the others. Sometimes, judging from Pearse's observations, this posing is certainly a part of courtship display, as in some of the tropical species, but at other times it is surely is not. It remains, with shelter-building, one of the mysteries.

**Hibernation:** On March 15 and 16, colonies of hibernating *pugnax* were examined near Atlantic City, New Jersey, in the salt marshes beside the causeway to Brigantine. The air temperature ranged from 35° to 42° Fahrenheit. The crabs were found, not on the open, spartina-grown flats, but in the foot-high, muddy banks of small creeks, near their mouths, where they opened into sandy-bottomed inlets. They could only have been submerged at occasional spring tides; and the open, weathered, half-frozen burrows, with no traces of tracks or feeding pellets, indicated both that they had not been covered at all and that the crabs had not been active for months. Probably the first activity was just occurring. I saw one female inside the mouth of her burrow, with her eyestalks elevated, although she was incapable of further movement.

The rest of the crabs were all between one and four inches below the surface, the burrows being dug obliquely into the banks, with some individuals lying almost exposed. With the least warming in the hands, or in a jar in the sun, the crabs became active enough to walk fairly rapidly, the young ones warming up first. Crabs were equally divided between the sexes, and were of all sizes, from early post-megalopal stages to large males. They were scattered without arrangement in reference to age or sex, with the young ones often among the deepest, since they had used the holes of large crabs. In the most populous spot, in a section measuring six by six by four inches (144 cubic inches), there were 11 crabs (four young, five adult females, two large males).

It is interesting to compare the shallow excavations of these crabs with Gray's report (1942) that the much larger *minax* hibernates below the frost line. Probably the

latter species, which is often found in almost fresh water, is more subject to freezing and is also less hardy than *pugnax*, which lives in strongly brackish districts.

***Uca minax* (LeConte, 1855).**

(Text-fig. 1b).

**References:** *Gelasimus minax* LeConte, 1855, p. 403.

*Uca minax*, Rathbun, 1918, p. 389; pl. 137.

**Range:** Massachusetts to Texas. Colombia.

**Supplementary Specific Characters:** A typical Group 2 *Uca*, more closely related to *pugnax* than to *mordax*. Like *pugnax*, in supplementary characters (p. 218) except as follows: spoon-tipped hairs of merus of second maxilliped with spoons exceedingly slender, apparently never more than 10 in number, well developed spoons even fewer; central groove of ischium of third maxilliped exceptionally shallow and slender, curving basally to meet inner groove; gape in minor cheliped sometimes extending only to distal part of serrations; female always with large genital tubercle; tip of abdominal appendage of male as in figure.

**Color:** (Not observed in bright sunlight, so omitted here; for general color notes, consult Gray, 1942).

**Display:** The following notes were made on a single, very dark day (July 4), and are not regarded as more than a partial description. Crab rears back on last two or three ambulatories so that carapace is vertical. Major cheliped extended diagonally up, to about half maximum stretch. This position may be held for minutes. In apparently full display, the cheliped is further extended diagonally up to maximum stretch, swiftly, without jerking, then brought down to half-way point or a little below, but not to flexed resting position, in three to five (usually four) decided jerks. Meanwhile the minor chelae perform similar but often completely unsynchronized motions (that is, often the major is going up as the minor comes down). Sometimes the middle ambulatories are elevated during display, as in others of the group. Movement is slow—that is, the jerking portion alone may take two or three seconds.

***Uca pugilator* (Bosc, 1801-2).**

(Text-fig. 1c, d).

**References:** *Ocypoda pugilator* Bosc, 1801-1802, p. 197.

*Uca pugilator*, Rathbun, 1918, p. 400; pl. 141; pl. 160, fig. 2.

**Range:** Massachusetts to Texas; Haiti.

**Supplementary Specific Characters:** Apparently basically related both to Group 4 (in display and minor cheliped) and Group

5 (in spoon-tipped hairs and abdominal appendage of male). Spoon-tipped hairs on merus of second maxilliped numerous, strongly developed; sometimes as many as 200 may project beyond inner margin of merus, with half as many more non-projecting short ones; in other individuals there is a total of only about 150, arranged in about 10 rows on inner third of merus throughout up to four-fifths of its length. Ischium of third maxilliped with central groove broad, shallow, parallel to inner groove, dying out at beginning of posterior half. Minor chelae with a few strong, jagged, median teeth, and very narrow gape. Sub-orbital region short, triangular, naked except near anterior margin. Abdominal appendage of male with well developed arm (see figure). Female without genital tubercle.

**Color:** Males, in full display: Carapace creamy white, entire cheliped buffy to creamy white, with base of fingers apricot; at other times, merus is yellowish or apricot. Manus and chelae of minor cheliped also creamy white. Eyestalks and ambulatories usually slightly darker, dirty white or buffy, as are underparts, except third maxilliped. Merus of ambulatories on anterior side likely to be darkest. Adult females almost or quite as light as displaying males. Just before assumption of this lightest phase, both sexes usually go through a stage showing a bright purple spot in middle of cardiac region.

**Display:** Much faster and more energetic than that of *pugnax*, except when the latter is extremely excited: *pugilator* in full display habitually waves at the rate of slightly more than one to the second. The crab starts with body elevated, meral-carpal joint of major cheliped elevated, the chelae tips obliquely lowered, touching ground; cheliped is then raised obliquely up and out, crab stretching meanwhile to extreme tip-toe. The ambulatories, unlike those of *pugnax* and others, are not elevated nor kicked outward at all, except for a rare, obviously accidental elevation of a leg with an especially high stretch. The cheliped is held a fraction of a second at peak, then returned to position, without ever a trace of jerking either on way up or way down. When the crab is greatly excited, the cheliped is not lowered quite to ground after display, nor does he sink so low on the ambulatories; likewise, there is no pause in the rest position, so that the accent comes at elevation of cheliped. Four or five of these peak displays follow each other in a series. Minor cheliped makes weak corresponding gesture. Both pairs of chelae remain practically closed throughout. The crab often remains in one spot, more rarely moves several steps to the side.

TABLE I.

	<i>pugnax</i>	<i>pugilator</i>
Woods Hole, Mass. (Pearse)	July 4-15	First part Aug.
Woods Hole, Mass. (Bumpus)	—	Early June.
Cold Spring Harbor, N. Y. (Swartz & Safir)	At height in mid-Aug.	July 6 to early Aug.

The above is the usual display, but there is an additional sequence reserved for specially excited crabs, often when the female has been attracted to the hole of a male, just before he descends. At full breeding season, it occurs far more often, and sometimes without the noticeable stimulus of a female, than earlier. This excited behavior superficially resembles the curtsy of *pugnax*, but is completely distinct in the means by which it is brought about: It is a rapping gesture made by a tattoo of the flexed cheliped against the ground, as is found in Group 4 crabs, including *cumulanta* and *oerstedii* and culminating in *saltitanta*. The ambulatories take no part in the rapping, and in its less complete stages it is only a quivering of the cheliped.

Another courting behavior sequence was noticed several times in this species, exactly as in *cumulanta* in Venezuela under similar conditions. A male, having attracted a female's attention enough to stop her somewhere near his hole, dodged down into it after frantic waving in the usual way. Also as usual, the female did not follow, but simply remained motionless where she was. Whereupon the male emerged and rushed several inches or more away from the hole on the opposite side from the female, mounted a tiny elevation, and displayed again vigorously, once or twice. Then, holding his cheliped high in the air, he raced again for the hole (toward her), bobbing

somewhat up and down, and vanished after rapping at the mouth of the hole. Once I saw this procedure followed by the prompt approach of the female, who thrust the legs of one side briefly down the hole, but then wandered off. The male emerged and repeated the same sequence, but this time she took no notice and went away.

#### GENERAL REMARKS AND CONCLUSIONS.

*Breeding Season:* Previously given breeding records for *pugnax pugnax* and *pugilator* in the field are shown in Table I. The dates refer to presence of ovigerous females.

It will be seen that there are some discrepancies. From my own incomplete observations, it seems likely that at least in the New York region, *pugnax* has two breeding seasons, one in early July, and one in August, whereas *pugilator* does not come into full breeding condition until August. Table II gives dates and localities for these conclusions. Only observations made on clear, sunny days at low tide are included.

My observations concerning the migration of ovigerous females to damper localities and general habits agree with those of Pearse and Swartz and Safir, etc. Also, my general remarks (1941, 1943) in regard to display in young males, behavior of females, etc., apply equally well to these northern species.

#### *Comparison of Displays and Their Rela-*

TABLE II.

March 15-16	Atlantic City, N. J.	Both spp. in hibernation. Residents say crabs never active here before last half of May. Temp. 32°-42° Fah.
May 15	Port Jefferson, N. Y.	Both spp. at mouths of holes, completely inactive; no signs of feeding; no waving or fighting; dull colors.
June	Various localities near New York City	Oral reports say no waving.
Early July	Same as above	Oral reports say waving beginning.
July 16	Greenwich, Conn.	<i>pugnax</i> waving and fighting sporadically; majority females ovigerous.
July 23-26	Pelham Bay Pk., N. Y.	<i>pugnax</i> less active than at Greenwich; <i>pugilator</i> waving strongly, but not at peak of display activity. Few ovig. females of either species.
July 29	Staten Is., N. Y.	<i>pugnax</i> displaying only slightly.
Aug. 5-7	Port Jefferson, N. Y.	<i>pugnax</i> again displaying strongly, but no ovig. females seen. <i>pugilator</i> at peak of display activity; a few females ovig.
Sept. 24-28	Mamaroneck, N. Y.	Oral reports say <i>pugilator</i> waving.

tion to *Phylogeny*: Anatomically, by the criteria used in previous tropical studies (Crane, 1941, p. 165 ff.) *pugnax* and *minax* belong to Group 2, along with *mordax*, *schmitti*, *brevifrons*, etc., while *pugilator* turns out to be quite distinct from any of the six groups so far recognized, although it has affinities with Group 4 and Group 5. When the displays of these three northern species are analyzed, they are found to follow closely this anatomical placing. Previously *mordax* and *pugnax rapax* were the only Group 2 members of which I had seen the display; both are "jerkers;" that is, the wave is broken on the down or up beat or both by a series of jerks. Both northern Group 2 forms, *pugnax pugnax* and *minax*, are likewise jerkers, (although the trait is poorly developed in *pugnax*), and include in their displays other Group 2 characteristics including slowness, kicking of the ambulatories and posing motionless with outstretched appendages. Likewise, both live primarily in typical, muddy, Group 2 habitats, varying chiefly in salinity, both are relatively phlegmatic, and both are dull in color. In addition, however, the display of *pugnax pugnax* has characteristics, including the curtsy, which, compared with the southern *pugnax rapax*, appear to be of more than subspecific importance and are another sign that, in evolution, a change in behavior may precede a change in structure. It may be noted here that there are also color differences between the two subspecies, especially in the presence of bright blue eye-stalks in the northern form.

The difference in the displays of the four known Group 2 "jerkers" may be tabulated as in Table III. Differences of rhythm, and special climactic behavior are omitted.

TABLE III.

<i>mordax</i> :	Cheliped jerks on both up and down strokes.
<i>minax</i> :	Jerks on down stroke only.
<i>pugnax rapax</i> :	Jerks on way up only (when displaying strongly; otherwise both on up and down strokes).
<i>pugnax pugnax</i> :	Jerks scarcely perceptible; can be on either up or down strokes, or on both.

Of all the fiddler crabs so far studied, *pugnax pugnax* appears to have the most variable, least definite display. Even in a colony apparently in full breeding condition, there is nothing of the constant flashing of chelipeds so characteristic of many tropical forms. Instead, small waves of display run through a colony, and, as has been pointed out, the individual variation is great. The unqualified success of the species in the north is attested by the enormous colonies

found; in this region, at least, their proper habitats are far more numerous than those of the other two species, and the individuals are correspondingly more abundant. It seems possible that in this adaptable, thriving species, the display may be tending to break down, perhaps through lessening need for it as a recognition device, since the vast majority of the colonies of *pugnax* are unmixed with individuals of either of the other species. The other probable use of display—that of stimulation—may be also less necessary here, because of climatic or other influences of which we at present know nothing. The other hypothesis is also possible, that the display of *pugnax* is primitive even compared with those of other primitive Group 2 crabs; nevertheless it must be remembered that it contains the specialized curtsy element.

*Uca pugilator*, the sand fiddler, on the other hand, is related basically to both the Group 4 "rappers," in its display and in the form of the minor cheliped, and to the Group 5 series, (which are noted for their adaptations to relatively dry habitats and for their apparently high type of nervous organization and great activity), in its spoon-tipped hairs and in the form of its abdominal appendage. In designing a phylogentic tree to include the Atlantic forms, at the present time I would place *pugilator* as a long offshoot near the base of the Group 4 stem, and the Venezuelan *cumulanta* from another, shorter, basal offshoot. *U. minax*, *pugnax* and *pugnax rapax* should all be placed near *mordax* and *schmitti* in Group 2. (See Crane, 1941, p. 166, text fig. 5).

*Importance of Unsolved Problems*: The fiddler crabs are especially worthy of detailed study because of two related facts. In the first place, they are at the summit of crustacean development in nervous organization. Secondly, in sexual dimorphism and complexity of display they rival the members of the remaining groups—all higher in the evolutionary scale—in which these characteristics reach their maximum, namely, salticid spiders, certain insects and some fishes, lizards and birds. In a comparative study of animal display, therefore, their position is fundamental.

There remain numerous unsolved problems concerning *Uca* behavior, the solutions of which are essential to a proper understanding of display. Any persons trained, or even sufficiently interested in natural history observation and experiment, could undertake some of these studies successfully, provided only that they could live close to a colony of fiddlers over a period of time. The geographical locality is of no importance. The following questions list only a few of the more obvious problems.

How do the males recognize females of



their own species? In some cases I have found that temporary, brief mistakes are made by both sexes. Is it by scent? I can find no constant, morphological sexual dimorphism in the first antennae which might indicate a higher development of the male sense of smell.

Is color vision developed in *Uca*, so that the brightening of male color in display may actually be of value in recognition and stimulation of the female? Or are the colors only by-products of endocrine activity and/or nervous excitement, of no practical value to the crab? Is brightness, as apart from color, of similar value?

What is the exact seasonal and individual development of display in each species? What is the significance of shelter-building? Of posing?

What is the use, presumably in feeding, of the spoon-tipped hairs on the merus of the second maxilliped? Why should they attain their greatest development in species inhabiting sandier localities?

What happens in the display of *pugnax* in localities, such as Key West and Havana, where the two subspecies intergrade (Rathbun, 1918, p. 398)? Through the study of details such as this, much light may be shed on the evolution of display in general.

Dembowski's (1925) observations of the "speech" and play of *Uca* should be continued.

Endocrine research in connection with the display of these crabs has yet to be started. The excellent laboratory work already done on eye-stalk hormones and their effect on color and moulting will form a useful foundation. Kleinholz (1942) gives a comprehensive survey of the work done, and includes a full bibliography.

It cannot be stressed too strongly that experiments and observations on the display of these animals must be conducted in the field, since laboratory animals do not behave naturally, either in color changes or breeding sequences. Of equal importance to the observer is the use of a large supply of patience, especially in studying the less active forms, such as those in Group 2. As has been pointed out in previous papers, the vast majority of all waving by individual crabs does not result even in attracting the attention of a female, much less does it culminate in mating. Yet it must not be decided on this account that it is of use only in demarcating territory or warning off rivals, as seems still to be the opinion of some writers. Anyone who has finally watched a pair of fiddlers in the later stages of courtship will be completely convinced of the ultimate use of waving.

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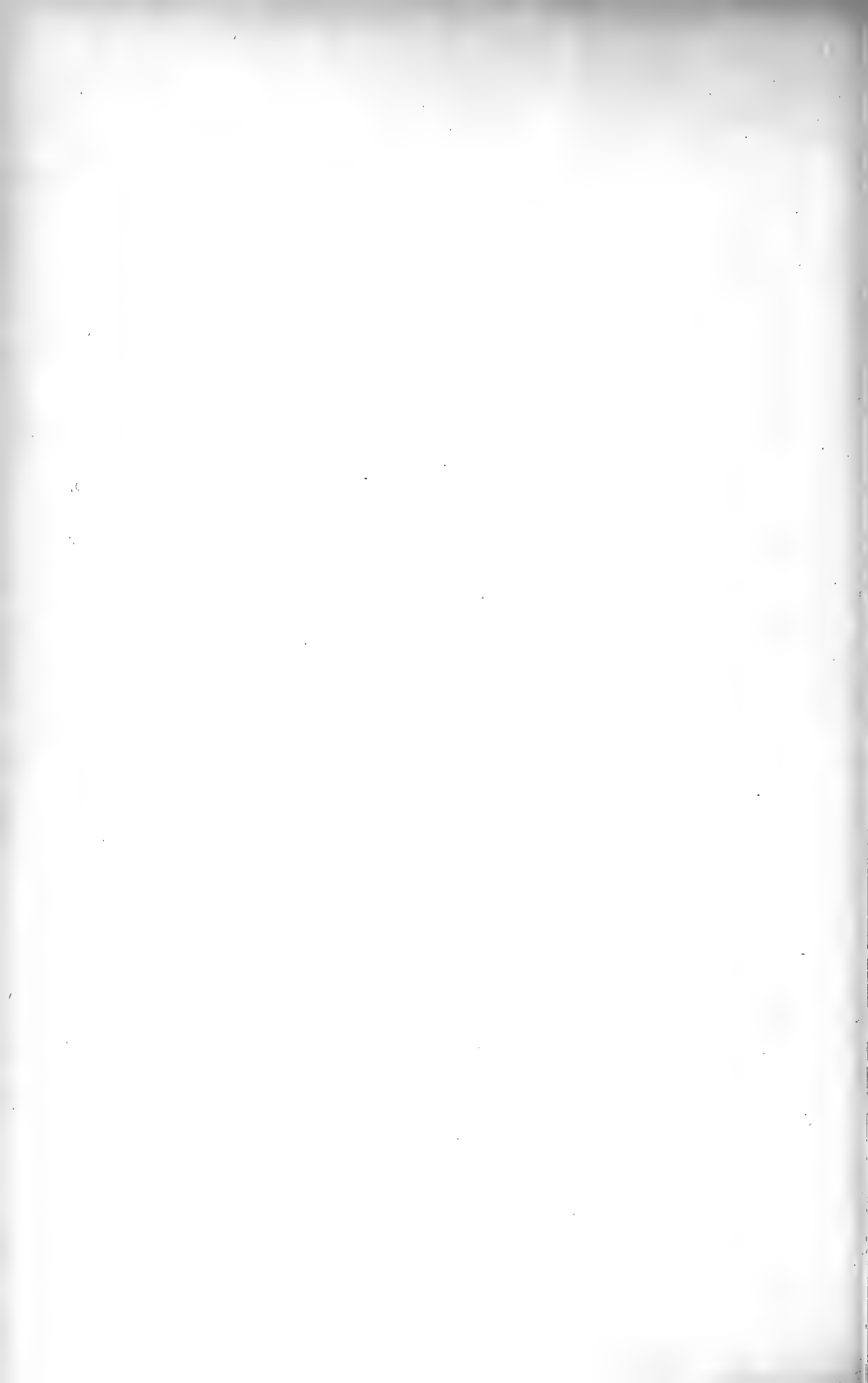
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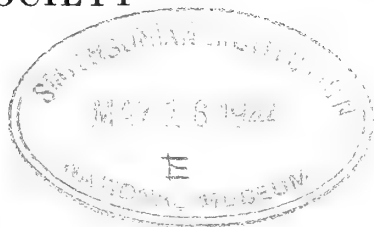
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## 1.

## New American Cerambycidae (Coleoptera) from British Guiana and Costa Rica.

W. S. FISHER

*Bureau of Entomology and Plant Quarantine, Agricultural Research  
Administration, United States Department of Agriculture.*

[This contribution is a result of two expeditions of the Department of Tropical Research of the New York Zoological Society, the British Guiana Expedition of 1924, and the Eastern Pacific Zaca Expedition of 1938. Both were made under the direction of Dr. William Beebe.]

In a small collection of cerambycid beetles received for identification, the following two new species were found.

*Stromatium kartaboensis*, sp. nov.

Narrowly elongate, subcylindrical, strongly convex above, subopaque, uniformly reddish-brown, legs and antennae slightly paler, sparsely, irregularly clothed with long, rather broad, recumbent, yellowish-white hairs, with a few long, fine, semi-erect hairs intermixed.

Head even, with a narrow, longitudinal groove extending from vertex to clypeus, flat between antennal tubercles, which are indistinct, transversely flattened between upper lobes of eyes; surface densely granulose, coarsely, shallowly, irregularly punctate, eyes deeply emarginate, separated from each other on the top by three times the width of upper lobe. Antenna slender, as long as body, unarmed, sparsely, finely punctate, sparsely ciliate beneath with long, semi-erect, yellowish-white hairs; first segment robust, cylindrical; third segment nearly twice as long as first; following four segments each shorter than third, and subequal in length to one another; last two segments missing.

Pronotum as long as wide, subequal in width at base and apex, widest at middle; sides arcuately rounded; disk strongly convex; surface densely, finely granulose and rugose, with three narrow, longitudinal, glabrous spaces on disk, extending from apex to base.

Elytra three times as long as pronotum, at base subequal in width to pronotum at middle; sides parallel from humeral angles

to near tips, which are broadly subtruncate; disk moderately, uniformly convex; surface sparsely, coarsely, irregularly punctate, the recumbent hairs forming more or less distinct vittae along sutural margins.

Abdomen beneath sparsely, finely punctate; last visible sternite broadly rounded at apex. Prosternum coarsely, transversely rugose, sparsely, indistinctly punctate; prosternal process very narrow between coxal cavities, arcuately declivous posteriorly. Mesosternum rather narrow between coxal cavities. Legs sparsely clothed with long, semi-erect and recumbent, yellowish-white hairs; femora unarmed at apices, anterior and middle pairs slightly flattened, expanded at middle, posterior pair slender, subcylindrical; tibiae slender, cylindrical, not expanded at apices.

Length 9-10 mm., width 2.25-2.5 mm.

*Type locality*: Kartabo, Bartica District, British Guiana.

*Type*: In the United States National Museum. Paratype in the collection of the Department of Tropical Research, New York Zoological Park. Type No. 56773; Paratype No. 241016.

Described from two specimens (one type) collected at the type locality, April 8-11, 1924, by William Beebe.

This species resembles *Elaphidion nanum* Fabricius, but it differs from that species in being uniformly reddish-brown and more slender, in having a different arrangement of the pubescence on the dorsal surface of the body, the antennae unarmed, with the third segment nearly twice as long as the first, the intermediate coxal cavities open externally, and the prosternal process very narrow between the coxal cavities.

*Anatinomma brevicornis*, sp. nov.

Elongate, subcylindrical, moderately convex above, slightly shining, yellowish-brown, except head, pronotum, basal region and lateral and sutural margins of elytra, underside of body, and tips of femora, which are reddish-brown, sparsely, uni-

<sup>1</sup> Contribution No. 682, Department of Tropical Research, New York Zoological Society.

formly clothed with short, recumbent, yellowish or whitish hairs, with numerous long, erect hairs intermixed.

Head even, flat between antennal tubercles, which are smooth and feebly elevated; surface coarsely, deeply, confluent punctate; eyes slightly emarginate, coarsely granulated, strongly projecting outward, separated from each other on the top by the width between antennae. Mandibles robust, broad, arcuate at apices; right mandible acute at apex; left mandible slightly truncate, depressed at apex for insertion of tip of right mandible. Maxillary and labial palpi subequal in length, last segment of each broadly triangular. Antenna short, extending to base of pronotum, unarmed, outer segments slightly flattened; first segment robust, slightly arcuate beneath; third segment subequal in length to first; following segments, except eleventh, each shorter than third and subequal in length to one another; eleventh segment slightly longer than tenth, oblong, broadly rounded at apex.

Pronotum as long as wide, slightly wider at apex than at base, widest at middle; sides slightly rounded, more strongly converging posteriorly; disk even, strongly, uniformly convex; surface coarsely, deeply, densely punctate at middle, confluent punctate at sides. Scutellum densely clothed with recumbent, whitish hairs.

Elytra nearly three times as long as, and distinctly wider than, pronotum; sides parallel from humeral angles to near tips, which are separately shallowly emarginate, with a long, acute spine at outer angle; disk moderately, uniformly convex; surface densely, coarsely, deeply, uniformly punctate,

the punctures slightly smaller toward apices.

Abdomen beneath sparsely, indistinctly punctate; last sternite broadly rounded at apex. Prosternum feebly, transversely rugose, coarsely, shallowly punctate. Anterior coxae contiguous, the cavities open posteriorly. Middle coxal cavities closed externally. Mesosternum narrow between coxal cavities, arcuately declivous anteriorly. Legs moderately long; femora feebly flattened, slightly clavate, unarmed at apices; tibiae slender, subcylindrical, not carinate, slightly expanded at apices.

Length 21 mm., width 6 mm.

*Type locality:* Golfito, Gulf of Dulce, Costa Rica. No. 38,544, *Zaca* Expedition, Department of Tropical Research, New York Zoological Society. March 8, 1938.

*Type:* In the United States National Museum, No. 56774.

Described from a single specimen, sex undetermined, received from William Beebe.

This species differs from the description given for *Anatinomma alveolatum* Bates in having the antenna only extending to the base of the pronotum, with the intermediate segments cylindrical and the third segment longer than each of the following segments, and the anterior coxae contiguous.

Bates (*Trans. Ent. Soc. Lond.*, 1892, pp. 150-151, pl. V, Fig. 8) erected *Anatinomma* for *alveolatum*, a new species from Mexico, placing it in the group *Piezocerides* of Lacordaire, but stating that this genus does not exactly fit into any of the numerous groups instituted by Lacordaire in his *Genera des Coléoptères*.



## 2.

Cerambycidae (Coleoptera) of Caripito, Venezuela.<sup>1</sup>

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## INTRODUCTION.

The family Cerambycidae has always been a great favorite with collectors. The beetles of this family are very numerous, and at least 25,000 species have been described. These are distributed over the greater part of the world, except in the extreme cold regions where there is very little plant life. The immature forms live in the twigs, branches, roots and trunks of various kinds of plants and trees. In the tropics the species are very numerous, and since many of these are restricted to certain host plants, there remain many undescribed forms in these regions.

The family is composed of beetles of diverse forms, including some of the smallest and largest beetles, are often brilliantly colored and often mimic members of various other families of Coleoptera, particularly the Lampyridae and Chrysomelidae, and also numerous wasps and bees of the order Hymenoptera. Many of the species are nocturnal in their habits, whereas others are found during the warmest part of the day frequenting flowers or running over the surface of their host plants.

A collection made at Caripito, Venezuela, contains 42 species, belonging to 37 genera. Nine of the species are new to science. All the specimens were collected at Caripito by William Beebe and his associates during 1942.

The types of the new species, through the kindness of Dr. Beebe, have been deposited in the collection of the United States National Museum, at Washington, D. C.

## Subfamily PRIONINAE.

*Strongylaspis corticaria* (Erichson).

*Ergates corticarius* Erichson, 1848, Schomb. Reise, III, p. 571.

One specimen, May 25.

This species is recorded from Mexico,

<sup>1</sup> Contribution No. 683, Department of Tropical Research, New York Zoological Society.

southward through Central America to Guiana, and in the West Indies is known from Cuba and Jamaica.

***Stenodontes (Mallodon) dasystomus* (Say).**

*Prionus dasystomus* Say, 1823, *Jour. Acad. Nat. Sci. Phila.*, III, p. 326.

Nine specimens, April to September.

Say described this species from the lower part of the Missouri River, but the species is distributed throughout the southern part of the United States, Mexico and Central America to the northern part of South America. Lameere places this species in the subgenus *Mallodon*.

***Macrodonia cervicornis* (Linnaeus).**

*Cerambyx cervicornis* Linnaeus, 1758, *Syst. Nat.*, ed. X, p. 389.

One specimen, no date.

This species has been recorded from Cayenne and the Amazon region.

***Callipogon (Enoplocerus) armillatus* (Linnaeus).**

*Cerambyx armillatus* Linnaeus, 1767, *Syst. Nat.*, ed. XII, p. 622.

Sixteen specimens, April to September.

This species has been recorded from Cayenne, Paraguay, Argentina, and the Amazon region. Lameere placed it in the subgenus *Enoplocerus* Serville.

***Pyrodes (Esmeraldo) auratus* (Linnaeus).**

*Cerambyx auratus* Linnaeus, 1758, *Syst. Nat.*, ed. X, p. 395.

One specimen, August 4.

This species is recorded from Guiana, Bolivia, Peru, Ecuador and the Amazon region. It is quite variable, and a number of varieties have been described, principally on the basis of color; and since the color varies in the two sexes, it is very difficult to use these varietal names unless a large series of specimens is available from the same locality.

**Subfamily CERAMBYCINAE.**

***Achryson surinamum* (Linnaeus).**

*Cerambyx surinamum* Linnaeus, 1767, *Syst. Nat.*, ed. XII, p. 632.

Four specimens, April 26-29 and May 4.

This species is widely distributed, extending from the southern part of the United States to Argentina in South America and from nearly all the West Indian islands. The posterior black marking on each elytron is variable in shape. It is usually V-shaped but is frequently divided into three small spots and sometimes represented by only a single spot.

***Brasilianus* Jacobson.**

*Brasilianus* Jacobson, 1924, *Rev. Russe Ent.*, XVIII, p. 238.

*Hamaticherus* Serville, 1834, *Ann. Soc. Ent. France*, III, p. 15.

Jacobson proposed *Brasilianus* for *Hamaticherus* Serville (1834), not Germar (1824), and designated *Cerambyx batus* Linnaeus as the genotype. Nine species have been described from northern South America, only two of which are represented in the collection.

***Brasilianus batus* (Linnaeus).**

*Cerambyx batus* Linnaeus, 1758, *Syst. Nat.*, ed. X, p. 390.

Two specimens, April 19 and May 11.

This species was described from "Indies," probably from a mislabeled specimen. It has been recorded from Surinam and northern Brazil. This species is uniformly brownish-black, with the palpi and tarsi brownish-yellow.

***Brasilianus plicatus* (Olivier).**

*Cerambyx plicatus* Olivier, 1790, *Enc. Méth.*, V, p. 299.

Two specimens, April 6.

This species has been recorded from Cayenne and Brazil. The head, pronotum and underside of the body are brownish-black; the antennae, palpi, tibiae, tarsi and elytra, reddish-brown; and the elytra have narrow, black, lateral margins.

***Eburia albolineata*, new species.**

Narrowly elongate, pale brownish-yellow, except mandibles, lateral and dorsal tubercles on pronotum, margin around eburneous spots on elytra, apical spines on elytra and middle and posterior femora, and prosternum, which are black or reddish-black.

Head transverse in front, deeply, transversely grooved behind clypeus, feebly, longitudinally grooved, and concave between antennae, sparsely, coarsely punctate, densely clothed with moderately long, recumbent, whitish hairs, nearly concealing the surface; antennal tubercles moderately elevated, widely separated, broadly rounded at apices; eyes deeply emarginate, separated from each other on the top by about the width of upper lobe. Antenna slender, slightly longer than body, densely clothed with short, recumbent, whitish hairs, with numerous long, erect hairs on underside of basal segments; first segment robust, slightly clavate, flattened on top and bottom near base, densely, shallowly punctate, two-thirds as long as third segment, which is slightly longer than fourth; fourth to tenth segments subequal in length; eleventh segment slightly longer than tenth.

Pronotum as wide as long (not including lateral tubercles), subequal in width at base and apex; sides sinuate, broadly rounded at middle, with a long, slender, acute, black tubercle; disk slightly uneven, with two

smooth, black, conical tubercles in front of middle, and a narrow, smooth, median space behind middle; surface finely granulose, finely, densely punctate, densely clothed with moderately long, recumbent, whitish hairs, concealing the surface. Scutellum densely pubescent, slightly transverse, broadly rounded at apex.

Elytra at base slightly narrower than pronotum at middle (not including lateral tubercles); humeri not elevated; sides nearly parallel from base to near apices, which are separately obliquely subtruncate, with a short concolorous sutural spine, and a long, black spine at outer angle; surface densely, coarsely punctate basally, more sparsely punctate toward apices, rather densely, uniformly clothed with short, recumbent, whitish hairs, which are denser along lateral and sutural margins; each elytron with two long, narrow, eburneous spots, the inner spot slightly constricted at middle, extending from base to behind middle, the outer spot extending from middle to near apex of elytron and narrowly separated from inner spot along middle of elytron.

Body beneath densely, finely granulose, densely, uniformly clothed with short, recumbent, whitish hairs; last abdominal sternite broadly subtruncate at apex; middle and posterior tibiae and femora long, slender, the latter each armed with a long, black spine on inner margin at apex; mesosternum tuberculate between middle coxae.

Length 20.5 mm., width 5 mm.

*Type locality*: Caripito, Venezuela.

Described from a single specimen, probably a female, collected May 16.

Type in U. S. National Museum, No. 56662.

This species seems to be intermediate between *Erosida* and *Eburia* but fits better into the latter genus. In general appearance it resembles the species of *Erosida* in being narrowly elongate and in having the long, eburneous spots on the elytra, but differs from the species of that genus in having distinct tubercles on the pronotum, and the third segment of the antenna longer than the fourth segment. *Eburia albolineata* differs from all the described species of these two genera in having the mesosternum distinctly tuberculate between the middle coxae.

***Eburodacrys pilicornis*, new species.**

Rather narrowly elongate, uniformly pale brownish-yellow, except mandibles, dorsal tubercles on pronotum, margins around eburneous spots on elytra, and apical spines on middle and posterior femora, which are black or reddish-black.

Head transverse in front, transversely, arcuately grooved behind clypeus, shallowly, longitudinally grooved between antennae,

coarsely, densely foveolate-punctate, sparsely clothed with short, erect and recumbent, inconspicuous hairs; antennal tubercles moderately elevated, widely separated, and obtusely rounded at apices; eyes deeply emarginate, separated from each other on top by twice the width of upper lobe. Antenna slender, about one and one-half times as long as body, densely clothed with long, erect hairs, outer segments also clothed with short, recumbent, whitish hairs; third and fourth segments longitudinally sulcate; first segment rugose and foveolate-punctate, robust, slightly flattened on top and bottom near base, sides nearly parallel, two-thirds as long as third segment, which is slightly longer than fourth, the following segments becoming gradually shorter to eleventh segment, which is slightly longer than tenth.

Pronotum slightly wider than long, subequal in width at base and apex; sides sinuate, slightly rounded at middle, with a short, obtuse, concolorous tubercle; disk slightly uneven, with two oblong, smooth, black tubercles in front of middle; surface coarsely, densely punctate, transversely rugose between dorsal tubercles, sparsely clothed with long and short, erect and recumbent, inconspicuous hairs. Scutellum small, transverse, broadly rounded at apex.

Elytra at base subequal in width to pronotum at middle (including tubercles); humeri not elevated; sides vaguely converging from base to near apices, which are separately broadly rounded, with a very small, concolorous spine at outer angle; surface sparsely, coarsely, irregularly punctate, sparsely clothed with long and short, erect, yellowish hairs, and with numerous small, rasp-like teeth along sutural margins; each elytron with three elongate-oval, eburneous spots, one at base, a longer one at middle closer to sutural margin than other spots, and one at apical third.

Body beneath sparsely, finely punctate, more coarsely punctate on prosternum, sparsely clothed with short recumbent and long, semi-erect, yellowish hairs. Middle and posterior tibiae long, slightly flattened, sides nearly parallel. Middle and posterior femora flattened, each armed with a long, black spine on inner margin at apex.

Length 16.5 mm., width 4 mm.

*Type locality*: Caripito, Venezuela.

Described from a single specimen, probably a male, collected May 1.

Type in U. S. National Museum, No. 56663.

This species resembles *Eburodacrys sexmaculata* (Olivier), but it differs from that species in being more slender, in having the black tubercles on the pronotum more distinct and oblong, the eburneous spots (except median ones) more oval, and all surrounded by narrow reddish-black areas,

the apical spines on the elytra very small and concolorous with the rest of the surface, and the elytra with numerous small, rasp-like teeth along the sutural margins.

***Stizocera rubricollis*, new species.**

Strongly shining; head, pronotum, basal segment of antenna, underside of body, and femora in part reddish; elytra brownish-yellow, with sutural margins black; antennae (except basal segment of each), tibiae, tarsi, and bases of femora black.

Head deeply, transversely depressed behind clypeus, with a narrow, longitudinal, median carina, flat between antennal tubercles, which are widely separated, slightly elevated, and obtusely rounded at apices; surface glabrous, very sparsely, irregularly, indistinctly punctate; eyes deeply emarginate, separated from each other on the top by three times the width of upper lobe. Antenna twice as long as body, sparsely, shallowly punctate, sparsely clothed with short and long, semi-erect, yellowish hairs, segments 3 to 7 unispinose at apices, the spines on sixth and seventh segments very small; first segment robust, slightly clavate, feebly arcuate, one-half as long as third segment, which is subequal in length to fourth segment; eleventh segment slightly longer than tenth.

Pronotum slightly longer than wide, subequal in width at apex and base, widest at middle; sides slightly constricted near base and apex, with a short, obtuse tubercle on each side at middle; disk uneven, transversely depressed behind anterior margin, transversely flattened along base, with four feebly elevated tubercles, two in front and two behind, the posterior pair more widely separated than anterior pair; surface nearly glabrous, very sparsely, finely, irregularly, indistinctly punctate. Scutellum transverse, broadly rounded at apex, densely clothed with recumbent, whitish hairs.

Elytra at base slightly wider than pronotum at middle; humeral angles broadly rounded; sides gradually converging from base to near apices, which are separately subtruncate, with a long, acute, black spine at outer angle; surface sparsely, finely, shallowly punctate basally, becoming impunctate toward apices, sparsely clothed with very short, erect, inconspicuous hairs, with a few long hairs toward apices.

Body beneath sparsely, indistinctly punctate (except prosternum), clothed with a few inconspicuous, erect hairs at middle, densely clothed with long, recumbent, whitish hairs at sides; last abdominal sternite broadly subtruncate at apex, and sparsely clothed with long, erect hairs. Prosternum rather densely, coarsely punctate, sparsely clothed with semi-erect, whitish hairs; prosternal process narrow between coxae,

arcuately declivous posteriorly. Legs long, sparsely clothed with short, semi-erect, yellowish hairs; anterior femora slightly clavate, middle and posterior femora gradually expanded toward apices, each acutely bidentate at apex; tibiae longitudinally carinate. Length 20-24 mm., width 5-6 mm.

*Type locality*: Caripito, Venezuela.

Described from two specimens (one type) both collected at the type locality, the type collected May 4 and the paratype May 2.

Type in U. S. National Museum, No. 56664.

This species is allied to *Stizocera vanzvaluwenburgi* Fisher described from Puerto Rico, but differs from that species in being larger and not uniformly pale yellow.

***Pantonyssus erichsonii flavipes*, new variety.**

Strongly shining, brownish-yellow, except head, two basal segments of antenna, tips of elytra, and spines on posterior femora, which are black or reddish-black.

Length 17 mm., width 3.5 mm.

*Type locality*: Caripito, Venezuela.

Described from a single specimen collected May 4.

Type in U. S. National Museum, No. 56665.

This variety differs from the typical form of *Pantonyssus erichsonii* (White) in having the legs and antennae (except two basal segments of each) brownish-yellow.

Bates erected the genus *Pantonyssus* for two species, *Sphaerion erichsonii* White from Pará, Brazil, and *Pantonyssus nigriceps*, new species, from Rio Janeiro, Brazil, without designating either species as the genotype, so the writer is designating *erichsonii* (White) as the genotype of *Pantonyssus* Bates.

***Gnomidolon confusum*, new species.**

Brownish-black, except antennae, legs in part, and elytra at humeri and middle along lateral margins, which are reddish-brown, strongly shining; each elytron with an elongate oval spot on disk at basal third, a narrow fascia extending obliquely backward from sutural margin in front of middle to lateral margin behind middle, and the apex, yellowish-white.

Head opaque, very coarsely, shallowly, irregularly punctate, concave between antennal tubercles, which are rather strongly elevated, and broadly rounded at apices. Antenna slightly longer than body, sparsely clothed with long, erect hairs on underside, third segment distinctly longer than fourth; first segment robust, cylindrical, slightly arcuate, coarsely, shallowly punctate; third to eleventh segments longitudinally carinate, the apical two only slightly.

Pronotum cylindrical, twice as long as wide, transversely depressed near base and

apex, without dorsal or lateral tubercles; sides nearly parallel, slightly constricted near base; surface smooth, impunctate, clothed with a few erect, inconspicuous hairs. Scutellum densely clothed with white hairs.

Elytra distinctly wider than pronotum, slightly, transversely flattened on middle third; sides arcuately expanded behind middle, apices separately transversely truncate, with a short, acute tooth at each outer angle; surface coarsely, rather densely, shallowly punctate basally, the punctures becoming finer toward apices, and with rows of sparse, rather long, erect, whitish hairs.

Body beneath indistinctly punctate, rather densely clothed with short, recumbent, whitish hairs, with a few long, erect hairs intermixed on abdomen; intermediate coxae separated. Legs sparsely clothed with long, erect hairs; femora gradually expanded toward apices, the middle and posterior pairs bispinose at apices, the spines equal in length, short, acutely angulated at apices, posterior pair bispinose at apices, the outer spine much longer than inner one; tibiae distinctly longitudinally carinate.

Length 10 mm., width 2.25 mm.

*Type locality*: Caripito, Venezuela.

Described from a single specimen collected April 1.

Type in U. S. National Museum, No 56666.

The markings on the elytra of this species resemble those on *Glyptoscapus cicatricosus* Aurivillius, but it differs from that species in having the segments of the antenna distinctly longitudinally carinate, and the first segment of the antenna without a cicatrix at the apex.

#### *Compsa vana* (Thomson).

*Ibidion* (*Compsibidion*) *vanum* Thomson, 1867, *Physis*, I, p. 151.

One specimen, March 26.

This species was described from Cayenne, but has also been recorded from Guatemala.

#### *Ibidion* Serville.

*Ibidion* Serville, 1834. *Ann. Soc. Ent. France*, III, p. 103.

This genus contains 84 described species. The species are badly confused and some of the forms described in this genus may belong to allied genera. Although many species have been described from northern South America, only two are represented in the collection, one of which is new to science.

#### *Ibidion binoculatum* Linsley.

*Ibidion binoculatum* Linsley, 1935, *Rev. Ent.*, Rio de Janeiro, V, p. 484, fig. 1.

One specimen, May 1.

This species was described from San

Salvador, but other specimens have been examined from Maracay, Venezuela, which do not differ from the type. The species is robust, of a uniform yellowish-brown color, and each elytron has an oval, eburneous spot, margined with black, in front of the middle.

#### *Ibidion beebei*, new species.

Elongate, moderately robust, strongly shining, uniformly reddish-brown; each elytron with two oblong, yellowish-white spots on disk, one arranged longitudinally in front of middle, the other obliquely at apical third, the spots partially surrounded by a dark brown color.

Head strongly transverse, glabrous, and uneven in front, narrowly, longitudinally depressed between antennal tubercles, which are slightly elevated and obtusely rounded at apices; surface indistinctly punctate; eyes coarsely granulate, globose, and not distinctly emarginate. Antenna slender, about as long as body, unarmed, sparsely ciliate beneath with long, erect hairs; third to ninth segments longitudinally carinate; first segment rather robust, cylindrical, slightly arcuate, abruptly thickened at apex, about two-thirds as long as third segment, which is nearly twice as long as fourth, the following segments subequal in length to one another.

Pronotum slightly longer than wide, vaguely narrower at apex than at base, widest at middle; sides unarmed, slightly constricted near base and anterior margin, feebly, broadly rounded at middle; disk convex, transversely flattened along base, feebly, broadly, transversely concave behind anterior margin, and with two small, erect, acute, approximate tubercles at middle; surface glabrous, impunctate. Scutellum elongate-triangular, broadly rounded at apex, densely clothed with short, recumbent, whitish hairs.

Elytra much wider than pronotum, moderately convex; sides parallel anteriorly, broadly, feebly expanded behind middle, tips separately, shallowly emarginate, not spinose; surface coarsely, sparsely punctate basally, the punctures becoming finer toward apices, very sparsely clothed with long, erect, brownish hairs.

Body beneath indistinctly punctate, with a few long, erect hairs on median part, densely clothed with short, recumbent, whitish hairs along sides; last abdominal sternite broadly rounded at apex. Legs sparsely clothed with long, semi-erect, brownish hairs; femora strongly clavate toward apices, unarmed at apices; tibiae longitudinally carinate.

Length 14 mm., width at base of elytra 3.5 mm.

*Type locality*: Caripito, Venezuela.

Described from a single specimen collected June 2.

Type in U. S. National Museum, No. 56667.

This species differs from the description given for *Ibidion bituberculatum* Serville in having the antennae and legs uniformly reddish-brown, and without a yellow spot at the tips of the elytra. It differs from the other species of this genus known to the writer in having the elytra expanded posteriorly and the eyes not distinctly emarginate.

***Cyllene cayennensis*** (Castelnau and Gory).

*Clytus cayennensis* Castelnau and Gory, 1835, *Monogr. Clytus*, p. 10, pl. III, fig. 9.

Three specimens, April 4 and August 2.

This species was described from Cayenne and has also been recorded from Nicaragua.

***Neoclytus guianensis*** (Castelnau and Gory).

*Clytus guianensis* Castelnau and Gory, 1835, *Monogr. Clytus*, p. 22, pl. V, fig. 26.

One specimen, March 6.

This species was described from Cayenne and has been reported from Paraguay, but there is some doubt about the record of this species from the latter locality.

***Chrysoprasis viridis***, new species.

Rather strongly shining; head and pronotum dark green, with a more or less distinct violaceous tinge; elytra dark green, with sutural and lateral margins violaceous blue; scutellum, prosternum, mesosternum, metasternum and anterior and posterior femora violaceous blue; abdomen red; antennae, posterior legs, anterior and middle tibiae, and tarsi black.

Head flattened in front, narrowly, arcuately grooved behind clypeus, with a narrow, longitudinal, median groove; surface glabrous, coarsely, densely, uniformly punctate. Antenna extending to tip of abdomen, opaque, sparsely ciliate beneath; first segment robust, cylindrical, two and one-half times as long as wide, coarsely, densely punctate; third to seventh segments armed on inner margins at apices with a short spine; third segment nearly twice as long as fourth segment, the following segments slightly longer than fourth, and subequal in length to one another.

Pronotum vaguely flattened on top, distinctly wider than long, widest at middle; sides uniformly, arcuately rounded; surface finely, densely foveolate-punctate, rather densely clothed with short, recumbent, black, inconspicuous hairs. Scutellum triangular, acutely rounded at apex.

Elytra at base slightly wider than pronotum at middle, slightly flattened on disk; sides parallel, broadly subtruncate at apices, rounded at sutural angles; surface densely, finely punctate, more finely punctate

along sutural and lateral margins, the intervals densely, finely granulose, rather densely, uniformly clothed with short, semi-erect, inconspicuous, whitish hairs, which are blackish toward lateral margins.

Abdomen beneath finely granulose, finely, sparsely punctate, sparsely clothed with rather long, semi-erect, whitish hairs. Prosternum finely, transversely rugose, densely clothed with long, erect, inconspicuous hairs. Metasternum coarsely foveolate-punctate, sparsely clothed with long, semi-erect, whitish hairs. Legs slender, finely, densely punctate, sparsely clothed with short, semi-erect hairs; middle and posterior tibiae bispinose at apices; middle and posterior femora acutely bidentate at apices, the posterior pair extending to tip of abdomen; posterior tarsi as long as tibiae, the segments densely pubescent beneath.

Length 13 mm., width 4.5 mm.

Type locality: Caripito, Venezuela.

Described from a single example collected April 24.

Type in U. S. National Museum, No. 56668.

This species is allied to *Chrysoprasis hypocrita* Erichson, but differs from that species in being more strongly shining, dark green, with a distinct violaceous blue tinge, and the sutural and lateral margins of the elytra violaceous blue; also in having the pronotum foveolate-punctate, and the elytra more coarsely punctured.

***Batus barbicornis*** (Linnaeus).

*Cerambyx barbicornis* Linnaeus, 1764, *Mus. Lud. Ulricae*, p. 68.

One specimen, No. 42130.

This beautiful black and orange beetle is widely distributed throughout northern South America, and has been recorded from Colombia, Ecuador, Peru, Bolivia, French Guiana, Dutch Guiana and Brazil.

***Trachyderes succinctus*** (Linnaeus).

*Cerambyx succinctus* Linnaeus, 1758, *Syst. Nat.*, ed. X, p. 391.

Two specimens, April 26 and May 4.

This is the most common species of *Trachyderes*. It is distributed from Costa Rica to Paraguay, and has been recorded from nearly all parts of that region. This shining reddish-brown beetle is rather uniform in color, but the transverse yellow fascia on the elytra varies in width, and sometimes has the margins black.

***Lissonotus equestris*** (Fabricius).

*Callidium equestre* Fabricius, 1787, *Mant. Ins.* I, p. 153.

One specimen, July 7.

This species was described from Cayenne, French Guiana, but it has been also recorded from British Guiana. In the typical



form of *equestris* the fascia on the elytra extends to the sutural margins and the sutural angles of the elytra are broadly rounded. Pascoe (*Trans. Ent. Soc. Lond.*, (2) V, 1859, p. 16) described a species from Para, Brazil, under the name of of *shepherdi*, stating that it closely resembles *Lissonotus equestris* but that the fascia on the elytra does not extend to the sutural margins nor are the sutural angles of the elytra rounded. The specimen from Caripito has the sutural angles of the elytra broadly rounded but the fascia does not extend to the sutural margins. When more material is available for study, *Lissonotus shepherdi* Pascoe, 1859, may prove to be a synonym of *Lissonotus equestris* (Fabricius), 1787.

***Lissonotypus fasciatus*, new species.**

Uniformly black, strongly shining, each elytron with a rather broad, transverse, median, reddish-yellow fascia, which does not extend quite to lateral margin; margins of fascia sinuate.

Head transverse and depressed in front, concave between antennal tubercles, which are slightly elevated, and obtusely rounded at apices, broadly depressed behind antennal tubercles; surface glabrous, coarsely, irregularly punctate. Antenna about as long as body, densely clothed with short, recumbent hairs, with a few long, erect hairs on underside; first segment short, robust, cylindrical, slightly expanded toward apex; third segment longer than any of the other segments; third to fifth segments feebly, longitudinally carinate; third to tenth segments broad, flattened, each strongly expanded and more or less serrate on outer margin at apex; eleventh segment oblong, acute at apex.

Pronotum globose, as long as wide, narrowly grooved along anterior margin and base, slightly narrower at apex than at base, widest at middle; base sinuate, without a median lobe; sides feebly arcuately rounded; surface glabrous, smooth, impunctate. Scutellum elongate-triangular, acute at apex.

Elytra distinctly wider than pronotum, strongly convex; sides nearly parallel, apices broadly rounded or subtruncate; surface glabrous, very sparsely, finely, irregularly punctate.

Body beneath sparsely, finely, irregularly punctate, sparsely clothed with short and long, semi-erect, inconspicuous hairs; last abdominal sternite broadly rounded and with a fringe of long, erect hairs at apex; prosternal process narrow, abruptly deflexed posteriorly, and vaguely tuberculate; mesosternum broadly concave anteriorly. Femora strongly pedunculate; middle and posterior pairs each with a short, acute

tooth on inner margin at apex. Anterior and middle tibiae feebly, longitudinally carinate.

Length 10.5 mm., width 4 mm.

Type locality: Caripito, Venezuela.

Described from a single specimen collected March 26.

Type in U. S. National Museum, No. 56669.

This species differs from *Lissonotypus brasiliensis* (Buquet) in having a transverse, median, reddish-yellow fascia on each elytron, and from *Lissonotypus quadrisignatus* (Buquet) in being entirely black, and in having only a single transverse, median, reddish-yellow fascia on each elytron. It resembles *Lissonotus equestris* (Fabricius) but differs from that species in having the pronotum narrower than the elytra and without a median lobe at the base, the third segment of the antennae subequal in length to the fourth segment, the elytra unarmed at the apices, the middle and posterior femora spinose at the apices, the tibiae unarmed at the apices, the posternal process narrow and slightly tuberculate, and the mesosternum concave in front.

***Megaderus stigma* (Linnaeus).**

*Cerambyx stigma* Linnaeus, 1758, Syst. Nat., ed. X, p. 395.

Two specimens, April 8 (No. 42160) and May 18.

This species is also widely distributed from Costa Rica to Brazil. It is a broad, flattened beetle, uniformly black except that each elytron has an oblique yellow fascia, which is variable in width, and frequently indicated by one or two small spots. This beetle does considerable damage to lead-sheathed aerial cables in Brazil.

**Subfamily LAMIINAE.**

***Tapeina* Serville.**

*Tapeina* Serville, 1825, Encycl. Meth. Ins., X, p. 545.

Five species have been described in this genus, one of them being represented in the Beebe collection. The males differ from the females in the remarkable lateral expansion of the head before the antennae and eyes, the front being laterally produced into processes or plates extending far beyond the antennal sockets, and even beyond the shoulders in some species. Species have been distinguished by the shapes of these plates as in the following table compiled from the descriptions.

**TABLE OF SPECIES.**

1. Body above bicolored; head and prothorax black, elytra reddish-brown. (Brazil) .....	<i>dispar</i> Serville
Body above unicolorous .....	2

2. Body above reddish-brown; elytra striate-punctate. (Chile).....*americana* Castelnau  
Body above black; elytra irregularly punctate ..... 3
3. Frontal plate of male broad, not strongly transverse, bilobed on top. (Colombia) .....*diadem* Gemminger  
Frontal plate of male narrow, strongly transverse, not bilobed on top ..... 4
4. Frontal plate of male elevated at sides. (Brazil) .....*coronata* Serville  
Frontal plate of male not elevated at sides. (Costa Rica, Mexico).....*transversifrons* Thomson

***Tapeina transversifrons* Thomson.**

*Tapeina transversifrons* Thomson, 1857, *Archives Ent.*, I, p. 44, pl. 7, fig. 3.

One specimen, July 4.

This species has been recorded from Mexico, Costa Rica, Panama and Venezuela.

***Parysatis nigritarsis* Thomson.**

*Parysatis nigritarsis* Thomson, 1868, *Physic*; II, p. 120.

Three specimens, April 15-16.

This species was described from Brazil and Colombia. The specimens from Colombia have the elytra paler brown than those examined from Brazil. It has been recorded from Mexico, Costa Rica and Bolivia.

***Hippopsis lemniscata* (Fabricius).**

*Saperda lemniscata* Fabricius, 1801, *Syst. Eleuth.*, II, p. 330.

Two specimens, June 14 and August 15.

This common species was described from "Carolina," but is distributed throughout the eastern United States, Mexico and Central America to Brazil, and breeds in the stems of various plants. The adult is long and very slender, with the antenna more than twice as long as the body, the pronotum is longer than wide, with two yellow pubescent vittae on each side, and each elytron has three yellow pubescent vittae, with the punctures arranged in longitudinal rows, and the tips acute.

***Onychocerus crassus* (Voet).**

*Cerambyx crassus* Voet, 1778, *Cat. Coleopt.*, II, p. 10, pl. 8, fig. 28.

Two specimens, May 8-11.

This species has been recorded from Brazil, Cayenne, British Guiana and Venezuela, and from Trinidad and Grenada in the West Indies.

***Acrocinus longimanus* (Linnaeus).**

*Cerambyx longimanus* Linnaeus, 1758, *Syst. Nat.*, ed. X, p. 388.

Two specimens, No. 42143; March 20; and April 1.

This large, well known beetle is distributed from Mexico to the southern part of Brazil and has also been recorded from the Barbados, British West Indies. It is the only species in the genus and is commonly known as the Harlequin Beetle. It is locally called "Mouche bagasse." It is a large flat beetle with very long antennae and front legs, especially in the males, with irregular pinkish, black and gray markings on the upper surface, and sharp spines at the humeral angles and sides of the prothorax.

***Oreodera glauca* (Linnaeus).**

*Cerambyx glaucus* Linnaeus, 1758, *Syst. Nat.*, ed. X, p. 390.

Two specimens, April 15, 27.

This species is distributed throughout Central and South America, and has been recorded from Puerto Rico, St. Lucia, Santo Domingo and the Bahamas. The adults are flat, variable in size, densely clothed with white, yellowish, or brownish-white pubescence, and the elytra have an irregular black spot along the lateral margins and a narrow, transverse, black fascia at the apical fourth.

***Oreodera jacquieri* Thomson.**

*Oreodera jacquieri* Thomson, 1865, *Syst. Ceramb.*, p. 542.

One specimen, May 5.

Up to the present time this species has been recorded only from Cayenne. The adult is flat, strongly attenuate posteriorly, densely clothed with brown pubescence; the prothorax has two large black tubercles on the disk in front of the middle; the elytra is tuberculate on the basal region, and the disk is covered with a large, white, pubescent spot, the sides of which are trilunate.

***Steirastoma breve* (Sulzer).**

*Cerambyx brevis* Sulzer, 1776, *Abgek. Gesch. Ins.*, p. 45, pl. 5, fig. 5.

One specimen, July 1.

Of the eighteen species assigned to *Steirastoma*, only one is represented in the collection. This species was described from Surinam, and has been recorded from Florida to the Amazon region, and in the West Indies from Trinidad and Grenada. It is reported as injuring "cocoa trees" in Venezuela and the West Indian islands.

***Acanthoderes circumflexa* Jacquelin Duval.**

*Acanthoderes circumflexa* Jacquelin Duval, 1857, *Hist. Cuba. Ins.*, p. 270.

One specimen, July 27.

This species is distributed from Mexico to Venezuela and is recorded also from Cuba.



***Acanthoderes nigricans* Lameere.**

*Acanthoderes nigricans* Lameere, 1885, *Ann. Soc. Ent. Belg.*, XXVIII, p. 110.

Four specimens, May 7-24.

This species was described from Venezuela and has been recorded also from Guatemala, Colombia and Brazil.

***Acanthoderes venezuelae*, new species.**

Female. — Elongate, convex, opaque, black, with head, pronotum and elytra ornamented with irregular, white, pubescent markings.

Head quadrate in front, concave between antennal tubercles, which are widely separated and slightly elevated, with a narrow, longitudinal, median groove, densely clothed with long, recumbent, white hairs, concealing the surface, except for a small space between antennal tubercles, a median spot on top of head, and a few coarse, glabrous punctures, the white pubescence forming a broad, Y-shaped spot on top of head; eyes deeply emarginate, separated from each other on top by about the width of upper lobe. Antennae slightly shorter than body, finely, densely punctate, densely clothed with short, recumbent, brownish hairs, narrowly annulated at bases of segments with white pubescence, not ciliate beneath; first segment short, robust, strongly clavate, flattened on underside at base, subequal in length to fourth segment, which is slightly shorter than third, the following segments gradually diminishing in length.

Pronotum nearly twice as wide as long, subequal in width at base and apex, widest at middle; sides angularly expanded at middle, with an acute tubercle on each side; disk uneven, narrowly, transversely depressed along base and anterior margin, with a small, glabrous, median spot behind middle; surface coarsely, very sparsely, irregularly punctate on disk and along base and anterior margin, densely clothed with short, recumbent, brown and white hairs, concealing the surface, the white hairs covering the middle third of pronotum, with sides of space sinuate and arcuately expanded on each side at middle. Scutellum broadly rounded at apex, densely clothed with short, white hairs, except at middle.

Elytra distinctly wider than pronotum, moderately convex, slightly uneven; sides nearly parallel from base to behind middle, then arcuately converging to tips, which are subtruncate; surface sparsely, rather coarsely, deeply, irregularly punctate, densely clothed with short, recumbent, brownish pubescence, concealing the surface. Each elytron ornamented with white pubescent markings as follows: a few small, inconspicuous spots on basal third, an irregular oblique fascia at middle, ex-

tending from middle of disk to sutural margin, and a large, triangular spot near apex, the margins of white pubescent spaces very irregular, and the large punctures in these spaces surrounded by brown pubescence.

Abdomen beneath densely, finely granulose, densely clothed with short, recumbent, whitish hairs, with a few long, erect hairs intermixed; last sternite longitudinally depressed at middle and subtruncate at apex. Legs short; femora strongly pedunculate, unarmed at apices.

Length 19 mm., width 7 mm.

*Type locality*: Caripito, Venezuela.

Described from a single specimen collected May 4.

Type in U. S. National Museum, No. 56670.

This species is allied to *Acanthoderes funeraria* Bates, but it differs from that species in being more slender, in having the antennal tubercles more strongly elevated, the eyes more narrowly separated on the top of the head, the white pubescence forming a broad Y-shaped spot on top of the head, the pronotum acutely tuberculate on each side and the middle third covered with a white pubescent spot, the margins of the scutellum clothed with white pubescence, a different arrangement of the white pubescent spots on the elytra, the underside of the body clothed with white pubescence, and the apical segments of the antennae longer and more slender.

***Lagochirus araneiformis* (Linnaeus).**

*Cerambyx araneiformis* Linnaeus, 1767, *Syst. Nat.*, ed. XII, p. 625.

Five specimens, February 26, March 14, May 5 and July 20.

This species is widely distributed from Florida to South America and in nearly all of the West Indian islands. It has also been recorded from Tahiti and Hawaii, where it probably has been introduced in commerce. It varies greatly in size and color markings.

***Leptostylus gibbulosus* Bates.**

*Leptostylus gibbulosus* Bates, 1874, *Trans. Ent. Soc. London*, p. 230.

One specimen, May 16.

This species was described from Venezuela and has been recorded also from Guatemala, Nicaragua and Panama.

***Probatius humeralis* (Perty).**

*Acanthocinus humeralis* Perty, 1830, *Delect. Anim. Artic.*, p. 91. pl. XVIII, fig. 8.

One specimen, June 1.

This species was described from southern Brazil, but it has also been recorded from the Amazon region and Cayenne.

***Hylettus vindex* Lacordaire.**

*Hylettus vindex* Lacordaire, 1872, Gen. Col., IX, p. 788.

One specimen, May 11.

Up to the present time this species is recorded only from Cayenne.

***Astyochus mucoreus* (Bates).**

*Astynomus mucoreus* Bates, 1872, *Trans. Ent. Soc. London*, p. 221.

One specimen, no date given.

This species was described from Nicaragua, but has been recorded also from Mex-

ico, Guatemala, Panama, Colombia and Venezuela.

***Colobothea pulchella* Bates.**

*Colobothea pulchella* Bates, 1865, *Ann. Mag. Nat. Hist.*, ser. 3, XV, p. 221 (separate, p. 152).

One specimen, May 15.

Of the one hundred and four species assigned to *Colobothea*, only one is represented in the Beebe collection. Up to the present time this species is recorded only from the Amazon region.

## 3.

The Metamorphosis of *Synodus foetens* (Linnaeus).

C. M. BREDER, JR.

American Museum of Natural History.

(Plates I &amp; II; Text-figure 1).

Although *Synodus foetens* (Linnaeus) is a well known and common fish along the south Atlantic coast of the United States and the postlarvae are recognized by most ichthyologists familiar with the region, it appears that only three partial descriptions of it have found their way into the literature: Nichols (1911), Beebe and Tee-Van (1928) and Norman (1935). The developmental stages are still to be described, although Sanzo (1915) gives a detailed description of the development of the similar *Synodus saurus* (Linnaeus) under the name of *Saurus griseus* Lowe. At the field laboratory of the New York Aquarium located on Palmetto Key, in Pine Island Sound, Florida, postlarval specimens may be taken irregularly at night lights at the head of the laboratory dock, at least during June and July. Such larvae are practically sub-leptocephali in form and are readily distinguished from Isospondyli larvae, also present, in the possession of six bilaterally paired and ventro-laterally placed internal dark blotches. Otherwise the general similarities of these postlarvae are in keeping with their evident affinities to the Isospondyli.

Both the young and adult of the *Synodus foetens* are common along the Florida west coast. Specimens in our collection have been taken at the following places.

LOCALITY	DATE	STANDARD LENGTH IN MM.	
Palmetto Key, north shore.	4/2/39	34-40	Recently transformed.
Boca Grande Pass.	4/28/39	29-31	Postlarval.
Palmetto Key, laboratory dock.	6-7/42	29-31	Postlarval.
Fort Myers.	3/2/43	33	Postlarval.

The egg of *Synodus saurus*, according to Sanzo (1915), measures 1.21 mm. in diameter and has a cluster of very small oil droplets and a very narrow perivitelline space. The only unknown egg taken in our

tow-net operations which even remotely resembles this is one of 1.2 mm. in diameter with a single small oil globule and a larger perivitelline space. We doubt if this is the egg of *Synodus foetens* and it seems likely that we have not taken it in our tows.

Laboratory work on this material was carried on in the Department of Animal Behavior of the American Museum of Natural History. Miss A. M. Holz, of that department, kindly prepared the cleared and stained material and made the microscopic sections necessary to the understanding of certain features of the specimens.

The transition of postlarval fishes to the adult form may proceed with extreme regularity and slowness or with considerable rapidity, in some cases amounting to practically an explosive change. We know of no case in which such a change is effected with greater rapidity than that of the planktonic postlarvae of *Synodus foetens* transforming to the bottom-dwelling adult form.

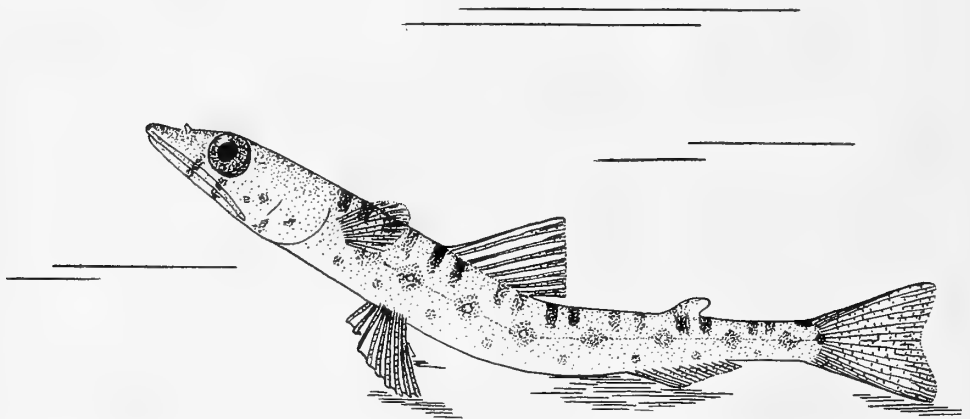
In connection with other matters, successful efforts were made to establish various Isospondyle postlarvae in aquaria during the summer seasons 1940, 1941 and 1942, see Breder and Krumholz (1943). Among them a single *Synodus foetens* postlarva was successfully established in a small aquarium of standing water. This specimen was captured and placed in the aquarium about 10:00 p.m. on June 19. At this time it was of glass-like transparency except for its black eyes and the six characteristic black patches. It was active and thoroughly planktonic in behavior and gave no hint of transformation. Nevertheless, by 8:00 a.m. the next morning, it had taken up residence on the bottom and showed a pale pattern on its back similar to that of the adult. From this time on its behavior was indistinguishable from that of the larger specimens that are abundant in this locality. The next day it was removed to a dish and photographed from above. This picture is given in Plate I over June 21. Here the size is indicated. Naturally it was impossible to measure the

living fish direct, but others, still planktonic, which were preserved as caught, ranged from 29 to 31 mm. in standard length. Transformed young of 34 to 40 mm. in standard length have been taken as early as March 2. This fact and visual observation give no suggestion that this species shrinks prominently, if at all, during metamorphosis as do some Isospondyle larvae, as for example *Albula vulpes*, Hollister (1936 and 1939), or as is well known among the Apodes, in the case of the leptocephalus of *Anguilla*. Growth from here on was regular until the specimen was preserved on July 10. Two further photographs were made and are shown opposite their respective dates in Plate I. This series of three photographs of the same fish well indicates the increasing intensity of pigmentation and the lack of any recognizable pattern change, as well as the generally increasing opacity of the flesh. A considerably larger specimen was also photographed in identical fashion for comparison as to the dorsal aspect of the pattern. This is given in Plate II, Figure 3. Large specimens of nearly a foot, not uncommon in this region, showed essentially the same type of pattern, although Hildebrand and Schroeder (1928), writing of specimens from Chesapeake Bay, indicate that fish of this size in that locality lack the bars across the back of the younger specimens.

The feeding of this tank-reared specimen was vigorous and the lunges that it made at passing plankton objects were notably voracious. Unfortunately there are no data on its feeding while in the postlarval stage. As its size increased it took small fishes with

equal vigor and because the quantities may not have been sufficient, it is supposed that the speed of growth may have been less than normal. Four poses of the fish as seen resting on the slate bottom of the aquarium are shown in Plate II, Figure 2. As the fish became larger it would raise up with its body at an angle as it gave attention to some passing food object. Unfortunately it was impossible to get a satisfactory photograph of this striking but transitory pose. This bending of the body, sharply in a vertical plane, increased with age. The sketch shown as Text-Figure 1 was made on July 8. It represents the extreme flexure of this type, the vertebral column bending sharply just back of the dorsal fin. Large specimens between three and six inches in length have not been seen to bend in this fashion. Although they prop themselves on the pelvises and slightly arch the back in a smooth curve of large radius, under similar circumstances, they seem to be unable to bend as sharply as the newly transformed fish. This may be a purely mechanical circumstance subject to the greater thickening of the tissues due to the increase in absolute size.

Cleared and stained specimens of the size that bend freely in a vertical plane show no skeletal modifications at the point of flexure, the numerous centra and their processes being all similar in detail from far ahead to far posterior of this region. The only difference between the successive centra of this region is the usual gradual decrease in size caudad. At this stage the vertebrae are fully ossified. Even before transformation the centra are ossified although at this earlier time the processes



TEXT-FIG. 1. Pose of newly transformed *Synodus foetens* when about to strike at a food object passing overhead.  $\times 2.91$ . This sketch, which shows the extreme of the bending in a vertical plane of which these fish are capable, was made eighteen days after transformation from a planktonic postlarva. The fish at this time was a little over 30 mm. in standard length.

are not completely ossified to their tips, as they are after transformation.

In the translucent flesh of the young transformed and patterned fish, the dark internal patches are still distinct, but in preserved material it may be seen that they are becoming overlaid by dermal pigmentation as is indicated in Text-figure 1. This figure also shows the diamond-shaped spots along the lateral line that are beginning to appear, but which cannot be seen in the dorsal-view photographs, although they show plainly in Plate II, Figure 1. It is also to be noted in nearly all the illustrations that each alternate pair of the dark saddle-like marks on the back are much darker than those intervening.

Beebe and Tee-Van (1928) describe the location of the ventro-lateral blotches as follows: "These black pigment spots lie between the gut and the peritoneum, and they are considerably more adhesive to the outer layer of tissue. The spots are upright, broad ellipses with solid edges." Dissection of the present material showed that these pigment patches were in the lining of the peritoneum. They appear to be composed of a uniform dark layer of minute pigment granules, unlike the ordinary melanophore pigmentation of young fishes. In sectioning it was found that this pigment layer was soluble in acid alcohol (3 per cent. nitric acid in 70 per cent. alcohol) and is evidently chemically different from ordinary melanin which withstands such treatment. As indicated by Beebe and Tee-Van, the spots are nearly elliptical and have sharply delimited outlines at the ventral end of the partial ellipse. In adults the peritoneum is pigmented and brownish in color down to a little below the mid-line of the visceral cavity, below which it is unpigmented. The pigmentation stops abruptly in a practically straight horizontal line.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Growth of a single specimen of *Synodus foetens*, from transformation of a planktonic postlarva to date of preservation, including three scale photographs of the dorsal aspect showing changes in size and extent of pigmentation.

## PLATE II.

- Fig. 2. Four views of a specimen of *Synodus foetens* resting on the slate bottom of

an aquarium. Photographed thirteen days after abandoning planktonic life. This is the same fish shown in dorsal view in Plate I. The internal ventrolateral blotches may still be seen in some of these poses.

- Fig. 3. A larger specimen of *Synodus foetens* of 64 mm. in standard length, on the same scale as those in Plate I, showing the increase in pigmentation with growth as well as the essential retention of the original pattern.



FIG. 1.  
THE METAMORPHOSIS OF SYNODUS FOETENS (LINNAEUS).





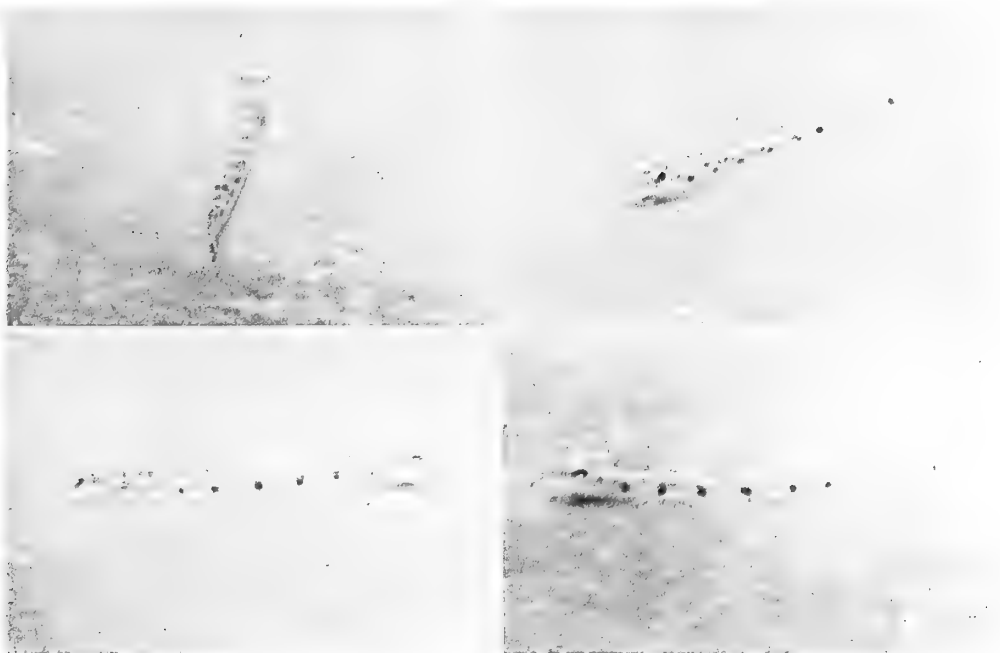


FIG. 2.

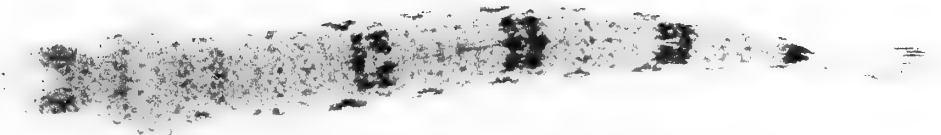


FIG. 3.

THE METAMORPHOSIS OF *SYNODUS FOETENS* (LINNAEUS).



## 4.

## A Revision of the Family Nectariniidae (Sunbirds).

JEAN DELACOUR

(Text-figures 1-14).

The members of the family Nectariniidae, the sunbirds, constitute one of the best characterized and most uniform groups among passerine birds. All are well adapted to their special mode of life, centering about flowers, on the nectar of which they feed as well as on the small insects attracted by them.

Sunbirds are by no means the only birds with such habits. The American hummingbirds (Trochilidae) are even more highly specialized in the same direction. Although far apart systematically—the Trochilidae belong to the Picarian order—and very different anatomically, sunbirds and hummingbirds show a further similarity in the brilliant metallic plumage worn by many species, especially the males. When the feathers are carefully examined, however, their gloss is found to be of a different character; so even this resemblance between the two families is superficial. They likewise differ so greatly in form, the hummingbirds having long, pointed wings and tiny feet, that even a layman will quickly learn to distinguish between them. Sunbirds, of course, are restricted to the Old World; hummingbirds to the Americas.

Some other passerine birds also feed partially or entirely flowers, notably the family Meliphagidae or honeyeaters, which inhabit the Australasian and Pacific regions, with one genus, *Promerops*, in South Africa as well. In general structure the Meliphagidae differ considerably from the Nectariniidae, particularly in the tongue. An important paper on the subject by Hans Scharnke will be found in the *Journal für Ornithologie*, LXXX, 1932, pp. 114-123. A translation of the part concerning the sunbirds (pp. 115-117) is as follows:

"I have examined the following species:

*Chalcostetha chalcostetha*, *Aethopyga siparaja*, *Aethopyga flavostriata*, *Cinnyris sericea*, *Cinnyris flammaxillaris*, *Cinnyris jugularis frenata*, *Cinnyris jugularis ornata*, *Cinnyris asiatica*, *Arachnothera flaviaster*, *Arachnothera chrysogenys*, *Arachnothera affinis modesta*, *Arachnothera longirostra*, *Anthreptes malaccensis*.

"The tongue of the Nectariniidae has a tubular shape only in its terminal two-thirds. The basal third is flat. The channel through which the nectar passes into the esophagus is formed by the turning up of the edges of the tongue until they meet in the midline. In the posterior part of this tubular section the rolling up is halted when the two edges touch the midline. This results in the formation of a single tube. Farther in front, the rolling up continues until two separate tubes are formed which lie side by side. How this operates can be visualized easily, if one takes a sheet of paper and rolls it up equally from the right and from the left until two parallel rolls are formed.

"The horny wall of this tube is formed only by the ventral part of the original tongue, as Moller showed in cross sections, and as is also the case in the Meliphagidae. The degeneration and gradual disappearance of the dorsal wall of the tongue can be observed well under the binocular.

"The two tubes of the tongue, which are closely attached along most of their length, are separated at the tip. This separation is caused in the above-listed species of *Chalcostetha*, *Cinnyris* and *Anthreptes*, by a ventral break along the midline, which permits the two tubes to become independent of each other. This permits the two new ventral edges of either side to roll upward until they meet the free dorsal edge. In this manner two complete separate pipes are formed.

"The tip of the tongue is formed quite differently in the species of the genera *Aethopyga* and *Arachnothera* examined by me. Their tongue agrees otherwise with that of the other species of Nectariniidae, but at the tip there is not a single median split, but rather two lateral ones. This produces two structures more groove-like than tubular, separated by an unpaired, flat, ventral centerpiece. The function of this piece may be to lie against the grooves in order to make them serve as pipes."

The sunbirds, in my opinion, are most nearly related, though not very intimately,

TEXT-FIG. 1. Tongue of *Nectarinia jugularis frenata*.  
× 4.

TEXT-FIG. 2. Tip of tongue of *Nectarinia jugularis frenata*. × 23.

TEXT-FIG. 3. Tip of tongue of *Aethopyga siparaja flavo-striata*. × 27.

TEXT-FIG. 4. Tongue of *Promerops cafer*. × 2.

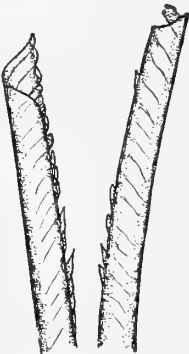
TEXT-FIG. 5. Tip of tongue of *Promerops cafer*. × 17.

TEXT-FIG. 6. Tip of tongue of *Myzomela sclateri*. × 10.

Text-figs. 1 to 6 after Scharnke.



1

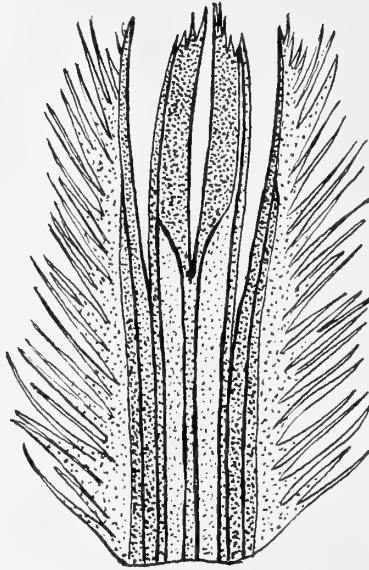


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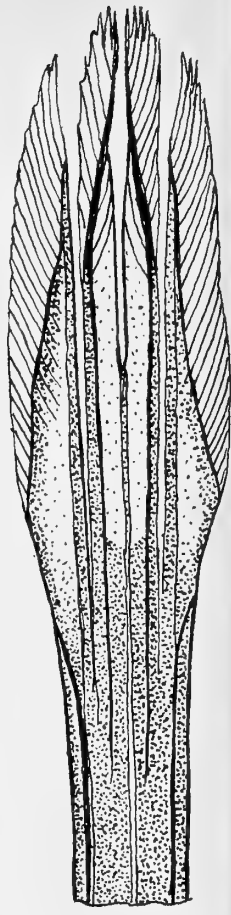


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to the Dicaeidae or flower-peckers, which inhabit tropical Asia, Malaysia and Australasia. These small birds are much less specialized than sunbirds, and have short bills, thin and curved only in some species; a few exhibit glossy feathering. Their tongues have a similar structure in general.

The Dicaeidae are less exclusively nectar- and insect-eaters. They feed principally on small berries, particularly on those of the various tropical mistletoes (*Loranthus*) amid which they are often found. Both sunbirds and flower-peckers have strong legs, short toes and sharp claws. An important point is that members of both families generally build elaborate, hanging, purse-shaped nests, although some aberrant Australian flower-peckers (*Pardalotus*) nest in holes.

On the other hand, the Dicaeidae are certainly allied to the so-called titmice of the *Remiz* group, which build pendulous nests, and through them to the long-tailed tits

(*Aegithalos* and allies). A small Himalayan bird, *Cephalopyrrhus flammiceps*, may provide a link between them. The only example I have ever seen alive, in Upper Laos during 1938, looked and behaved so like a *Dicaeum* that I mistook it for one until it had been collected. Examination in the flesh confirmed my impression of its affinities. *Cephalopyrrhus*, to be sure, nests in holes in trees; but since a few Dicaeidae have similar habits, this is no bar to placing it among them. I may state here that I consider *Remiz*, *Aegithalos* and allied forms too different from *Parus* and related genera for their inclusion in the family Paridae. They well deserve further study and revision.

The Nectariniidae and the *Remiz-Aegithalos* group of titmice all have ten conspicuous primaries in the wing, while many Dicaeidae have a minute and partly concealed first primary. As I have said when revising other families, I do not attribute any great importance to the reduction of the first primary.

The Zosteropidae, or white-eyes, likewise resemble the sunbirds, though less markedly. They form a compact group, well represented throughout the tropics of the Old World, and must have become differentiated at an early stage.

The suggestion has been made by Shelley ("The Birds of Africa," 1900, vol. II, p. 12) that *Neodrepanis* may be related to *Philepitta*, another Madagascan genus. He bases his statement on a certain similarity in colors and on the presence of an eye-wattle in the male. Such a relationship seems improbable, since *Philepitta* belongs to the Mesomyodian Passeres. The two species of *Philepitta* have brushy tongues, their bills are short and the size of the birds is much larger than that of any of the sunbirds. In habits, moreover, they have little in common. I do not agree with Bates' suggestion that the *Hylia prasina* may be a close relative of the sunbirds.

If we consider the Nectariniidae as a whole, we find that the family exhibits certain definite characteristics. It consists of small to very small passerine birds with long, thin, curved bills that in most genera show varying degrees of serration. I have examined under the microscope the bills of all the species represented in the American Museum of Natural History. The nostrils are oval, placed in a groove, and covered by an operculum. The tongue is tubular in its anterior two-thirds and split near the end; the "horns" of the hyoid apparatus are very long and well adapted to the protrusion of the tongue. Rictal bristles are wanting. The tarsus is strong and scutellate; the toes are short and stout, with sharp nails. The rounded wing has ten primaries; the third

to fifth are longest and the first is usually much reduced. The tail of twelve rectrices is square, rounded or graduated; the two central feathers are narrow and lengthened in the males of several species. The plumage is generally bright; metallic, and sometimes velvety in the males; it is usually dull in females. In the genus *Arachnothera*, and in several primitive species of *Nectarinia* and *Anthreptes*, metallic colors are absent, and both sexes are similar or only slightly different. On the other hand, the females of a small number of species of *Anthreptes* and *Nectarinia* have partly metallic plumage either similar to that of the males or a little less elaborate. In those that have no metallic colors, juvenile birds resemble females.

The males of a certain number of species have a dull off-season or eclipse plumage which replaces their brilliant dress after the breeding season. This must be a recently acquired character, and need not indicate close relationship, for it varies in closely allied forms. Males of many species, and females of some, possess bright pectoral tufts of lengthened, fluffy feathers, erectile during display and varying from yellow to red. They too are of slight systematic significance.

All sunbirds build the same type of long, purse-shaped nest, hanging from a bough or leaf of a tree, less often placed in a bush. It is more or less elaborate and generally provided with a porch-like projection above its lateral entrance. The eggs are always spotted or blotched, usually numbering two, sometimes more.

Sunbirds have sharp, metallic voices, and some sing fairly well. They are active and sprightly. Although many individuals, of several species, may gather in flowering trees, they are not truly sociable and males are extremely pugnacious in the nesting season. They inhabit primeval forests, park-like country, or dry jungle. A number of species have become familiar garden-dwellers; a few live only on high mountains. In general, and particularly in Africa, the very brilliant species are found in the more open situations, and only the duller ones may inhabit the shady, heavy forest.

In the present revision I recognize 106 species of sunbirds, distributed over the Ethiopian, Indo-Malayan and parts of the Australian regions. One species, *Nectarinia osea*, reaches Palestine and southern Syria; another, *Aethonyia gouldiae*, ranges as far north as central China. The latter migrates somewhat to the south in winter; otherwise most sunbirds make only local seasonal movements in search of flowers.

In such a compact family group only a small number of genera can properly be distinguished. Two Asiatic-Malaysian groups

are readily separable from all others by the distinctive structure of their tongues, and from each other by their bills and feet, as well as by the texture and pattern of their plumage: *Arachnothera* (9 species) and *Aethopyga* (13 species). The two species of *Neodrepanis* inhabiting the forests of eastern Madagascar are well characterized, too, by the large wattle surrounding the eye of males during the breeding season, and by their distinctive first primary, long and falcate.

It is difficult to group the remaining 82 species satisfactorily. The various characters, often not clear-cut, are combined in so many ways that I find it impossible to recognize more than two generic groups.

These characters, in the order of their importance, are as follows: length and form of bill, texture and pattern of plumage in both sexes, shape of tail, and pectoral tufts. Most of them cannot be used for generic division, as has too often been done thus far; but the comparative shortness and thickness of the bill does permit the placing of 16 species in the rather composite genus *Anthreptes*. This group undoubtedly represents a less advanced stage in specialization. All the remaining species (66) must be included in the large genus *Nectarinia*, with the bill thin, curved, and always longer than the head. Within both these genera, however, the bill varies greatly, often even among the races of a single species.

While the majority of species are easily referred to *Anthreptes* or to *Nectarinia*, a few are somewhat intermediate and offer difficulties. Such is the case with *Anthreptes reichenowi* and *A. anchietae*, in which the bills are rather long and thin for the genus, and with *Nectarinia seimundi*, often considered an *Anthreptes*, but in reality the most primitive member of *Nectarinia*. The case of the peculiar species *hypogrammica* is still more puzzling. Some of its subspecies (*lisetae*, for example) have the bill decidedly long as in *Nectarinia*, while in the nominate race it is shorter and could be regarded as that of an *Anthreptes*. The very special color pattern, general form and behavior have led me, however, to refer it to *Nectarinia*, with some misgivings.

Like other passerine families, the sunbirds have usually been studied not as a whole, but according to geographic distribution. Even Shelley, author of a very good monograph (1878), and Gadow (Cat. Birds Brit. Mus., Vol. IX, 1884) did not always appreciate the true affinities of the species of *Nectarinia*. In more recent years there has been a turn for the worse, and a number of unnecessary genera have been named and accepted.

The first cause of confusion was the unhappy custom of considering the shape of

the tail (square, graduated, or with elongated central rectrices) to be of generic importance. Yet this character was not even used consistently. No one, for example, has ever proposed the separation of *regia*, a species with graduated tail, or of *graueri*, a subspecies with such a tail, from their evident allies with square or rounded tails. The most specialized forms in many groups tend to develop a long, ornamental tail independently. The same progress is illustrated in the genus *Aethopyga*. Lengthened tails are found in numerous forms which otherwise show no great similarity in the plumage pattern of the two sexes, and which on the contrary are clearly related to different short-tailed birds.

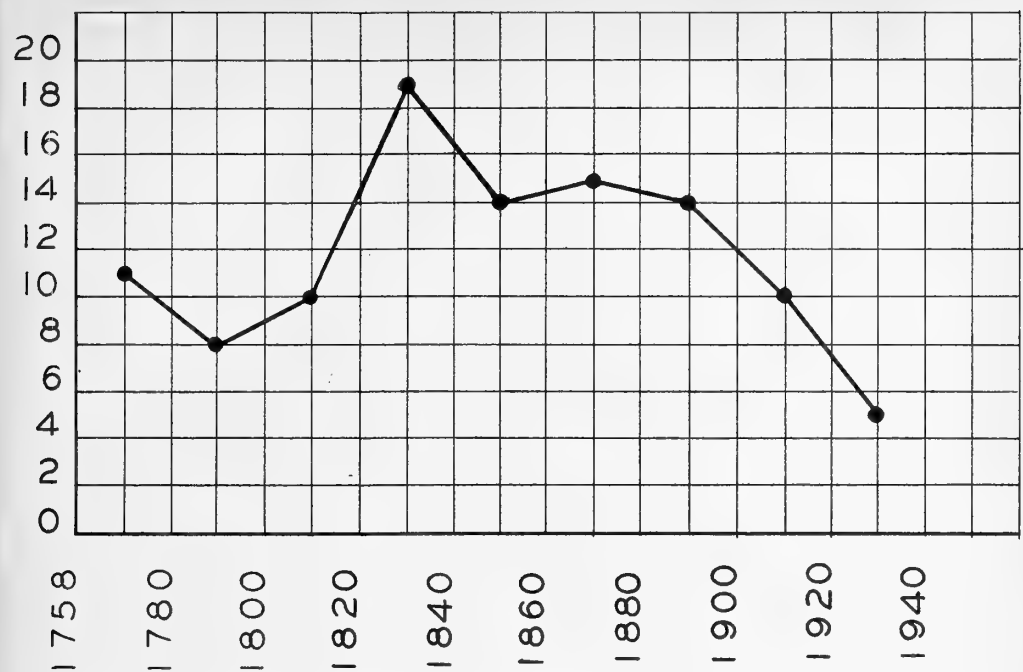
This observation disposes immediately of several genera currently recognized: *Cinnyris*, *Anthobaphes*, *Dreptes*, *Anabathmis* and *Chalcostetha*, all based merely on the shape of the tail. They must all be placed in the genus *Nectarinia*. It also permits us to consider the birds usually placed in the genus *Hedydipna* as an extremely specialized species of *Anthreptes*, and likewise *Eudrepanis* and *Urodrepanis* synonyms of *Aethopyga*.

The numerous species of the genus *Nectarinia* are distributed throughout the range of the family. *Nectarinia* differs from *Arachnothera* and *Aethopyga* in the structure of the tongue, from *Anthreptes* in having the bill longer than the head, from *Neodrepanis* by the absence of a wattle around the eye and the shortness of the first primary. It is possible, however, to base minor divisions of *Nectarinia* upon the pattern of the plumage; yet such groups are linked by intermediates in such a way that lines of division are hard to draw. They can only be considered as subgenera.

In the present study, as in previous revisions of other groups, I shall not attempt to review critically all of the subspecies, or their exact distribution. When necessary, I shall give briefly my reasons for their regrouping. The sequence of the species is perforce artificial, and the Text-figures will convey a better idea of their true relationships.

The number of genera has been reduced to 5, that of the species to 106, a conspicuous simplification and, I hope, an improvement on the systems previously adopted by other authors. Again, I consider as subspecies of one species all forms which differ only in degree of pigmentation or of proportion, and which replace one another geographically. Complete inter-gradation between races I do not regard as essential.

My work has been based on the large and excellent series in the collection of the American Museum of Natural History, under the care of Dr. Robert Cushman Murphy. Doctors James P. Chapin and Ernst



TEXT-FIG. 7. Dates of description of the 106 species of sunbirds recognized in the present list.

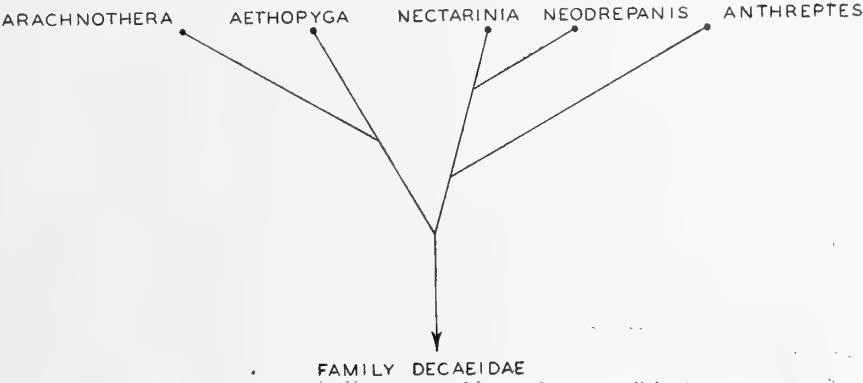
Mayr have as usual been of the greatest help, and have kindly read my manuscript. I thank them most sincerely.

My experience with sunbirds in life has been extensive. I probably have kept more species in captivity than any other aviculturist; and I have collected and observed many forms in the wild state, including a number not previously described, mostly in Indo-China but also in India, in Madagascar and in various parts of Africa. This should justify my endeavor to revise the family in the light of recent researches.

I. GENUS *Anthreptes*.

Tongue ending in two half-cylindrical lobes. Bill slightly curved, equal to the head or shorter. Nasal operculum naked. Mandibles finely serrated or only roughened. First primary short. Both sexes sometimes with metallic colors, or both without; or males with, and females without. Pectoral tufts present in all males except in *gabonica* and *platyura*, less often in females.

The plainest species, *gabonicus*, is olive brown above, whitish below, with a pale



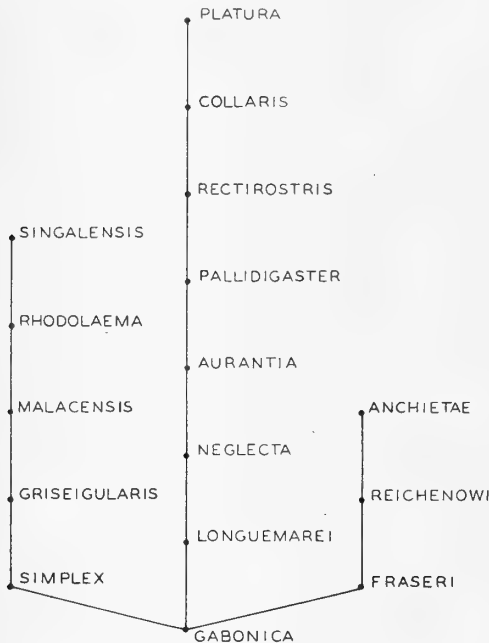
TEXT-FIG. 8. Genera of the Family Nectariniidae.

eyebrow; it probably represents the most primitive sunbird now existing. Other species can be divided into three groups: two African and one Indo-Malayan, as shown in the diagram. The less specialized forms of each group have a duller plumage and a longer tail. In the most elaborate species, *platura*, the two central rectrices of the male in breeding plumage are narrow and greatly elongated.

With the exception of two species (*gabonicus* and *fraseri*) all males show metallic colors. Except in *reichenowi*, *rectirostris* and *platura*, the females of all other African species have some metallic feathers, differing only slightly from the males in several cases.

In all the Indo-Malayan species, males have metallic feathering but females have none. In *simplex*, however, the metallic purple-blue is reduced to the forehead of the male.

*Anthreptes* is found over most of the range of the family, from Africa to the Philippines and Celebes. Some of the species inhabit rain forest, others, dry jungle and gardens.



TEXT-FIG. 9. Species of the Genus *Anthreptes*.

1. *A. gabonicus*. Brown Sunbird. Gambia to the Lower Congo, on the coast.
2. *A. fraseri*. Scarlet-tufted Sunbird. Upper Guinea to eastern Belgian Congo and Uganda.
3. *A. reichenowi*. Gunning's Sunbird. Coast of Kenya Colony to Portuguese East Africa (lower Zambesi Valley).

4. *A. anchietae*. Anchieta's Sunbird. Angola to Northern Rhodesia and Mozambique.
5. *A. simplex*. Plain-colored Sunbird. Malay Peninsula, southern Burma and peninsular Siam; Sumatra, Borneo, Nias and Natuna Islands.
6. *A. griseigularis*. Gray-throated Sunbird. Philippine Islands.
7. *A. malacensis*. Brown-throated Sunbird. Southern Burma, Siam and Indo-China; Malay Peninsula, Sumatra, Java, Philippines, Celebes and neighboring islands.
8. *A. rhodolaema*. Rufous-throated Sunbird. Tenasserim, Malay Peninsula, Sumatra, Borneo.
9. *A. singalensis*. Ruby-cheeked Sunbird. Burma, Indo-China, Siam, Malay Peninsula, Sumatra, Java and neighboring islands.
10. *A. longuemarei*. Violet-backed Sunbird. Savannas of the Ethiopian region from Senegal to Abyssinia, south to Angola, Mashonaland and Portuguese East Africa.
11. *A. neglecta*. Uguru Sunbird. Eastern Tanganyika Territory.
12. *A. aurantium*. Blue-backed Sunbird. Forested Cameroon, Gaboon and Belgian Congo.
13. *A. pallidigaster*. Moreau's Sunbird. Northeastern Tanganyika Territory.
14. *A. rectirostris*. Shaw's Sunbird. West Africa, from Gambia to Fernando Po and the Congo, Uganda and Usambara in Tanganyika Territory.
15. *A. collaris*. Collared Sunbird. The greater part of the Ethiopian region from Senegal and Kenya Colony south to eastern Cape Province.
16. *A. platura*. Pygmy Long-tailed Sunbird. Senegal, east across the Sudan to Philae on the Nile, Abyssinia, Eritrea, Somaliland and southwestern Arabia, south to the northern Congo and northern Uganda.

#### NOTES:

*A. axillaris*, from Uganda and the Belgian Congo, is certainly conspecific with *fraseri* from Fernando Po and West Africa, differing only in its gray instead of olive head.

*A. yokanae* Hartert (*Bull. B.O.C.*, XLI, 1921, p. 63, Rabai, N. of Mombasa) is either identical with or a very indistinct race of *A. reichenowi* Gunning (*Ann. Transvaal Mus.* 1, 1909, p. 173) from the lower Zambesi Valley, Portuguese East Africa. I could not examine the latter, but Grant and M. Praed share my opinion (*Bull. B.O.C.*, LXIV, 1943, pp. 11-12).



*A. griseigularis*, *A. malacensis* and *A. rhodolaema*, although very similar, must be considered separate species, as two of them coexist in many localities of Malaysia and the Philippines.

*A. singalensis* is certainly related to the three preceding species, which it closely recalls in its plumage pattern. But it appears to be a regressive species in that its bill is particularly short, almost straight, and devoid of real serrations, the edges of both mandibles being only roughened. I do not think, however, that such a character warrants the separation of this species in a special genus (*Chalcoparia*), even less in a special family, as Stuart Baker proposed (Fauna of Br. India: Birds, III, 1926, p. 368). It is much too near other *Anthreptes* in every other way. Serration is very variable in sunbirds, as the microscopic examinations of many hundreds of specimens has convinced me. It is fairly constant in each species, but only within certain limits. It can differ in closely allied forms. Such a character cannot therefore have much taxonomic meaning. A similar state of things is found in the African species of *Pycnonotus* of the subgenus *Andropadus* (cf. Revision of the Pycnonotidae, Zoologica, XXVIII, 1943, p. 18) to a much higher degree. All other species of *Anthreptes* have weak serrations, sometimes almost invisible, particularly in some specimens of *platura* and *malacensis*. The peculiar sunbirds of the genus *Neodrepanis*, long said to lack serrations, have in fact none on the upper mandible, but some very small ones on the lower. For all these reasons I include *singalensis* in the genus *Anthreptes*. I never found, as Stuart Baker asserts, that it differs in any way in habits from other sunbirds.

The question of the Violet-backed Sunbirds in East Africa has been discussed by J. Vincent (*Ibis*, 1936 pp. 72-74) and by R. E. Moreau (*Ibis*, 1937, pp. 335-337). It seems that the best solution is to recognize *A. neglectus*, in which the female possesses an entirely metallic mantle, as a full species, and to consider all other forms, including *orientalis*, as subspecies of *A. longuemareii*. It does not seem probable that the ranges of any of them really overlap. If they do, *orientalis* will have to stand as a full species.

I have not been able to examine specimens of *A. pallidigaster*, but from its description it seems to be not very far from *A. aurantia*.

*A. tephrolaema* is certainly a southern race of *A. rectirostris*, only with less yellow pigment.

*A. platura* is the most specialized species of the genus, but is fairly closely related to *A. collaris*, as shown by the color pattern of the males. The bill is very short and only

indistinctly serrated. As it is found in other genera of sunbirds (*Nectarinia* and *Aethopyga*), the lengthening of the tail of the male is but an extreme specific differentiation. *A. metallicus* is merely an eastern race of *platura*, with the purplish-blue color appearing on the breast and extending farther on the back.

## II. GENUS *Nectarinia*.

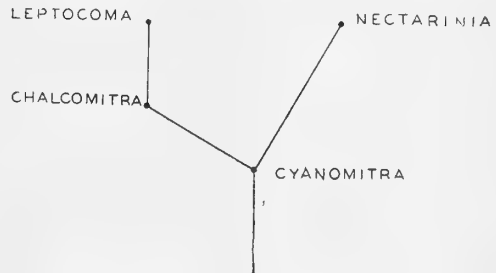
This genus, by far the largest of the family, differs from *Anthreptes* mainly in its longer and more curved bill. It is therefore more highly specialized and, containing a far greater number of species, it includes forms of more varied and elaborate color pattern. On the whole, however, it follows closely the same variations as *Anthreptes*.

In the majority of species the nasal operculum is naked, but in a small group it is covered to a varying degree with short metallic feathers like those of the forehead. The bill is always serrated, but more or less finely and deeply. It varies greatly in length and curvature, even in subspecies of the same species.

In the more primitive forms both sexes are dull and alike, as in *Anthreptes*. Only in a few slightly less primitive ones, females show metallic colors like the males, or are slightly duller. But in all the more advanced species which form the very great majority, males always possess metallic colors, while females lack them.

In *Nectarinia* the tail varies from short and square, with or without elongated central rectrices, to strongly graduated. Its length often varies greatly among races of the same species.

As I have noted above, it is possible to distinguish four subgenera in the genus *Nectarinia*; and in the larger of them, we can group species for practical purposes according to the plumage pattern of both sexes. The adoption of these minor groupings makes it easier to understand the particular relationships of a large number of species which, however, are not sufficiently differentiated to be considered as forming genera.



TEXT-FIG. 10. Subgenera of *Nectarinia*.

Subgenus **Cyanomitra**.

This subgenus is composed of primitive species which have several characters in common. The plumage of the more generalized forms is olive all over, darker above; then gradually there appear yellow or red pectoral tufts, metallic fringes to some feathers, and finally patches of metallic colors. But these solid patches are always dark purplish-blue or green, and they are confined to the head, throat and upper breast, one aberrant species of uncertain status (*hypogrammica*) showing purplish-violet on the nape and upper tail-coverts. Except for pectoral tufts, the only bright non-metallic color present is yellow; but brown, gray and olive are always dominant.

In the majority of species, females resemble males, but in four (*hypogrammica*, *hartlaubi*, *newtoni*, *cyanolaema*) they are almost as strikingly different as in the other subgenera. In *verticalis*, the female also differs from the male, but retains a metallic cap. These better evolved species resemble some of the more advanced groups. *N. cyanolaema*, although close to *verticalis*, plainly recalls *N. (Chalcomitra) fuliginosa* in both sexes, while *N. hartlaubi* and *N. newtoni* are not very far from *N. (Nectarinia) dussumieri* and *N. (N.) jugularis*. In the majority of species of *Cyanomitra*, however, the bill is proportionately coarser, broader and deeper at the base. But it never is so thickened as in *Anthreptes*. Pectoral tufts are present in males, except in those of *seimundi*, *batesi*, *hypogrammica*, *hartlaubi*, *newtoni* and *thomensis*. Females of *ursulae*, *verreauxi*, *reichenbachii* and *oritis* are also tufted. In *olivacea*, they have tufts or not, according to the subspecies.

All species of the subgenus *Cyanomitra* are African, with the exception of one from Socotra and one from Indo-Malaysia.

1. *N. seimundi*. Little Olive Sunbird. Liberia to Fernando Po, east to Uganda.
2. *N. batesi*. Bates's Sunbird. Fernando Po, southern Cameroon, and Belgian Congo.
3. *N. olivacea*. Olive Sunbird. Practically the whole Ethiopian region, in forests.
4. *N. ursulae*. Little Mouse-colored Sunbird. Fernando Po.
5. *N. verreauxi*. Mouse-colored Sunbird. South and East Africa, from eastern Cape Colony to Lamu Island.
6. *N. balfouri*. Socotra Sunbird. Socotra Island.
7. *N. hypogrammica*. Blue-naped Sunbird. Burma, Siam, Indo-China, Malay Peninsula, Sumatra, Natuna Is., Borneo.

8. *N. reichenbachii*. Reichenbach's Sunbird. West Africa, from Gold Coast to Gaboon and western Belgian Congo.
9. *N. hartlaubi*. Principé Sunbird. Principé Island.
10. *N. newtoni*. Newton's Sunbird. São Thomé Island.
11. *N. thomensis*. São Thomé Sunbird. São Thomé Island.
12. *N. oritis*. Western Blue-headed Sunbird. Highlands of Fernando Po and Cameroon.
13. *N. alinae*. Blue-headed Sunbird. Ruwenzori and mountains of the Kivu District.
14. *N. verticalis*. Green-headed Sunbird. Senegal to the Congo, Uganda, southwestern Tanganyika Territory and Nyasaland.
15. *N. cyanolaema*. Blue-throated Sunbird. West Africa from the Gambia and Fernando Po, east of Uganda.

## NOTES:

*N. seimundi* is undoubtedly the most primitive species of the genus, and one of the most primitive of the family. It has been considered an *Anthreptes*; but on account of its slender, rather long bill, of its similarity to *N. batesi*, and of its striking differences in proportions from the primitive *Anthreptes gabonica* and *A. fraseri*, it is preferable to place it in the present genus.

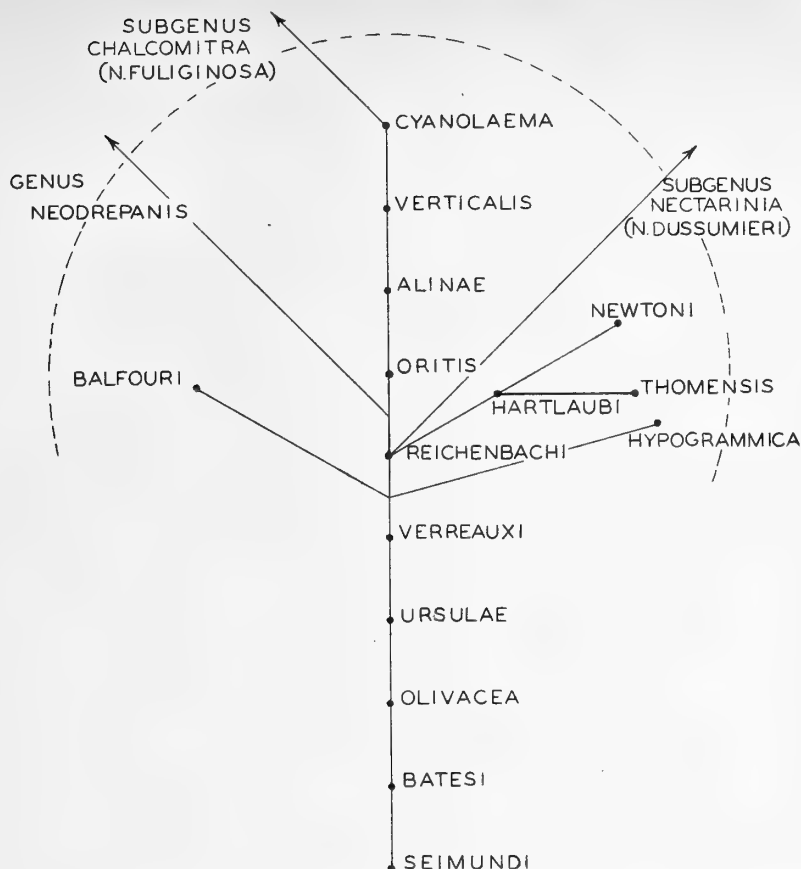
*N. batesi*, which is found in the southern Cameroon alongside *N. seimundi*, is so similar as to be difficult to distinguish. However, it has a slightly longer and more curved bill, is a little deeper in color, and the inner parts of its rectrices are darker. This is another case of two very closely allied species living in the same territory.

*N. ursulae* is an island representative of *N. verreauxi*, much smaller and approaching *olivacea* in its greenish back. I consider it a full species.

[The spelling of *verroxi*, being evidently an error in transcription of Verreaux's name, must be altered to *verreauxi*.]

*N. hypogrammica*, as stated before, is a very puzzling species, not closely related to any other. The place given it here is purely tentative. Because of its general coloration and of its apparently primitive nature, it fits better in *Cyanomitra* than in any other subgenus.

*N. balfouri* is also peculiar in its pale gray, streaked and spotted plumage, but the dark marks of its feathers seem to represent an alteration of a metallic pattern through adaptation to desert conditions. It is not really very different from other forms of *Cyanomitra*.



TEXT-FIG. 11. Species of the Subgenus *Cyanomitra*.

*N. hartlaubi* and *N. newtoni* are island representatives of *N. reichenbachii*, but they show further specialization in the very different plumages of the two sexes. They recall the color pattern of *N. jugularis*, from the Indo-Malayan-Australian regions.

*N. thomensis*, remarkable for its large size, long graduated tail and purple-edged plumage, represents a much transformed offshoot of the same group, the product of an early invasion. *N. newtoni*, very small and different in pattern, is probably a later invader of São Thomé which has evolved in an opposite direction.

The last four species: *oritis*, *alinae*, *verticalis* and *cyanolaema*, show a gradual evolution toward the more advanced groups.

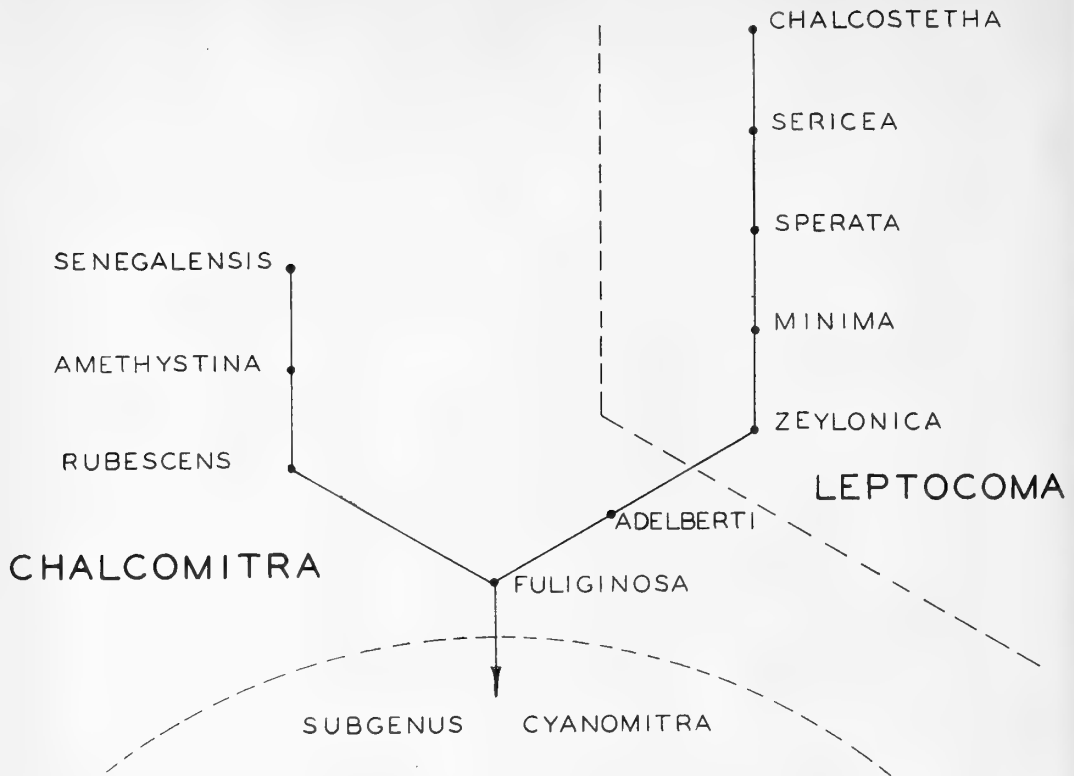
#### Subgenus *Chalcomitra*.

The sunbirds of this group are easily distinguished from all others by their rather long bill, short, square tail, long body, and by the general velvety brown or black color of their plumage. Metallic colors are confined to the crown, throat and chest, wing

and upper tail-coverts. Females are rather dark, with mottling or stripes on the breast. According to climatic conditions, they may or may not be tinged with yellow underneath. The nasal operculum is naked. The most primitive species, *fuliginosa*, has yellow pectoral tufts, in the male only. All five species are African.

16. *N. fuliginosa*. Carmelite Sunbird. West Africa from Senegal to the western Congo.
17. *N. rubescens*.\* Green-throated Sunbird. Fernando Po, Cameroon, Gaboon and N. Angola to Uganda and Kavi-rondo.
18. *N. amethystina*. Amethyst Sunbird. Southern and eastern Africa from Cape Province to Angola, northeastern Uganda and Lamu Island.
19. *N. senegalensis*. Scarlet-chested Sunbird. Savannas of the Ethiopian region, from Senegal to Eritrea and Somaliland, south to Natal.

\* Replaces *angolensis* auct.



TEXT-FIG. 12. Species of the Subgenera *Chalcomitra* and *Leptocoma*.

20. *N. adelberti*. Buff-throated Sunbird.  
West Africa, from Senegal to Nigeria.

NOTES:

The five species of the subgenus *Chalcomitra* are closely connected. The first three are certainly closer together than the other two, but still represent separate species.

The range of *N. senegalensis* covers practically all the suitable parts of the Ethiopian region. Its subspecies vary in their size, in the depth of their general color, going from smoky brown to black, in the tone of the scarlet of their chest, where the metallic blue middle bar of the feathers is more or less visible, and in the shade and extent of their metallic patches. These are confined to the crown, moustachial streaks, chin and upper throat in the majority of subspecies, but in others: *gutturialis*, *cruentata*, *hunteri*, the lesser wing-coverts are bright violet, and in the last-named, the rump and upper tail-coverts as well. Similar variations are found in *N. amethystina*. *N. cruentata* is merely the Abyssinian subspecies of *senegalensis* differing from the others in its black chin, and from most of them in its violet lesser wing-coverts, similar to those of *gutturialis*. *N. hunteri*, found in Somaliland

and the drier parts of southern Abyssinia and Kenya, west to northeastern Uganda, is also a subspecies of *senegalensis*, as its territory does not seem to overlap with that of any others. It differs most from *cruentata* in being blacker, in having the posterior part of the green crown shading into violet, the rump and upper tail-coverts violet blue, and in lacking the blue middle band to the scarlet feathers of the middle of the breast.

*N. adelberti*, a rare species, shows a definite affinity in its color pattern to *N. zeylonica* and so links this subgenus with the following one.

Subgenus *Leptocoma*.

This Indo-Malayan group of sunbirds is certainly related to the African *Chalcomitra*. Like them, the members have a great deal of velvety feathering, brown, black, or even red. Their metallic colors, never extensive, are confined to the crown, throat, upper breast, lower back, wings and tail, reaching the lower breast only in the most specialized species. The mantle and sides of the head are always velvety. They differ from *Chalcomitra* in several particulars; they are smaller and shorter; their bills are weaker;

the nasal operculum is covered with small feathers; their tail varies from short and square to rounded or graduated and fairly long.

The females are of a very different pattern, grayish-olive above, uniform yellow below, more or less pure, the throat being usually pale. In the majority of forms the head is gray and the throat white. Only one species (*N. chalcostetha*) shows pectoral tufts, in the male.

Sunbirds of the subgenus *Leptocoma* range from India and Ceylon to the Philippines, Celebes, the Moluccas, New Guinea and the Bismarck Archipelago.

21. *N. zeylonica*. Amethyst-rumped Sunbird. Ceylon and India, north to Bombay, Calcutta and Assam.
22. *N. minima*. Small Indian Sunbird. Ceylon and western India, north to Bombay.
23. *N. sperata*. Van Hasselt's Sunbird. Assam, southern Siam, southern Indo-China, Malay Peninsula, Sumatra, Borneo, Java, the Philippines, Celebes and neighboring islands.
24. *N. sericea*\*. Black Sunbird. Celebes, Moluccas, New Guinea and neighboring islands, Bismarck Archipelago.
25. *N. chalcostetha*. Macklot's Sunbird. Southern Burma, Siam and Indo-China; Malay Peninsula, Sumatra, Borneo, Palawan, Java and neighboring islands.

#### NOTES:

We have noted above the relative similarity in general pattern of *N. zeylonica* and *N. adelberti*.

I include in *N. sperata* all the forms usually referred to *N. braziliana*, and I also consider as conspecific *N. grayi* of Celebes. Peters (*Bull. Mus. Comp. Zool.* LXXXVI, No. 2, Nov. 1939, p. 121) had pointed out, quoting Chasen, that *braziliana* and *sperata*, together with *henkei* and *juliae*, constitute one species. The variations of the velvety portions of the plumage from black to maroon above, deep maroon to red and yellow below, with several combinations, are very interesting.

*N. sericea* is near *N. sperata* in its general pattern, but all the velvety parts of its plumage are always pure black. The metallic patches vary in hue with the numerous subspecies. Females are of the usual type, a few having a yellow instead

of a white throat, and an olive head instead of a gray one.

As to *N. chalcostetha*, it is just a long-tailed, more brightly colored form of this group, in which the metallic purple invades the whole breast and yellow pectoral tufts appear. The female resembles closely that of *N. sericea*, differing only in its longer, graduated tail and in its large size. It is a lowland species, common in rubber and coconut plantations.

#### Subgenus *Nectarinia*.

This large group includes all the species in which metallic colors are the most extensive, with no velvety feathers except in two species, *johannae* and *superba*, which have a maroon red band across the breast. The more primitive forms have the upper parts dull olive or brownish-gray, and the metallic color reduced to a purple patch on the throat and breast. It gradually invades the forehead, the crown, the back and the breast, and changes to various shades of blue, green, violet and coppery red, first dark and sombre, becoming brighter until, in the end, almost the whole plumage is glistening with iridescence.

Females are always dull-colored and differ slightly in pattern in the various groups. The strength, weakness, or absence of the yellow pigment varies even among geographical races and depends upon their damper or drier habitat.

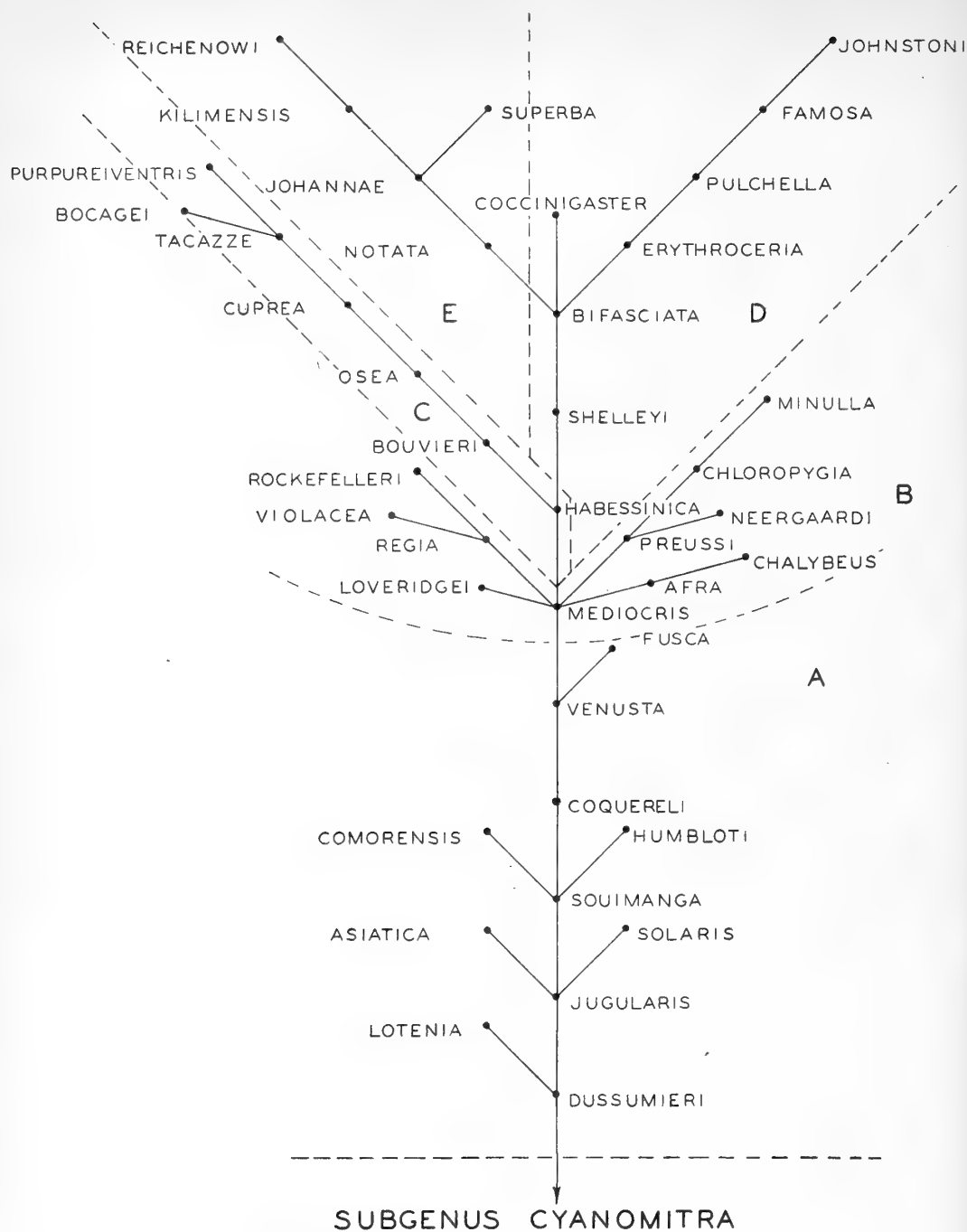
The tail may be short and square, or long, graduated, or with narrow and lengthened central rectrices; there are all sorts of intermediate stages. Long-tailed birds are found in different groups and represent the extremes of evolution in several lines, having no very close connection with one another. Size is variable, as are the length and curvature of the bill. Pectoral tufts are present in males of approximately seven-tenths of the species, never in the females, with the exception of one (*N. johnstoni*). *Nectarinia* occurs throughout the whole range of the family.

#### GROUP A.

Sunbirds of this group are small, square-tailed and the least brilliant of the subgenus. The most primitive males have metallic purple only on the throat and chest, breast gray or yellow and upper parts dull. The most specialized are metallic above and below down to the upper breast; but the colors are always dark, never very bright: purplish violet, copper, steel blue or bronze green. The feathers of the lower breast and abdomen are never shiny, varying from white and yellow to orange, brown and black; the upper tail-coverts are not enlarged.

\* *Nectarinia sericea meyeri* (*Hermotimia meyeri* Sharpe, *Handl. Gen. Sp. Birds*, V, p. 43, 1909), new name for *scapulata* Meyer and Wigglesworth, *Abh. Mus. Dresden*, 1896, p. 16, Celebes (East), is preoccupied by *Nectarinia jugularis meyeri* (*Cinnyris frenata meyeri* Hartert, *Nov. Zol.* IV, p. 156, 1897; N. Celebes).

I propose for it the new name: *Nectarinia sericea wigglesworthi*.

TEXT-FIG. 13. Species of the Subgenus *Nectarinia*.

Females have gray or olive upper parts, light gray or yellow under parts, either uniform or slightly mottled, but never striped or spotted. The males have pectoral tufts, which are absent in females.

Species of Group A are found all over the range of the genus.

26. *N. dussumieri*. Seychelles Sunbird. Seychelles Islands.

27. *N. lotenia*. Loten's Sunbird. Ceylon and Southern India, north to Ratnagiri and Madras.

28. *N. jugularis*. Olive-backed Sunbird. Bur-

ma, Andaman and Nicobar Islands, Siam, Indo-China, Hainan, southern China, Philippines and neighboring islands, Malay Peninsula, Sumatra, Java, Borneo, Lesser Sunda Islands, Celebes, Moluccas, New Guinea and neighboring islands to the Solomon Islands, N. Australia.

29. *N. solaris*. Orange-breasted Sunbird. Lesser Sunda Islands.
30. *N. asiatica*. Purple Sunbird. Afghanistan, Baluchistan, India, Ceylon, Assam, Burma, southern Siam and Indo-China.
31. *N. souimanga*. Souimanga Sunbird. Madagascar, Assumption and Aldabra Islands.
32. *N. humbloti*. Humblot's Sunbird. Great Comoro and Moheli Islands.
33. *N. comorensis*. Anjouan Sunbird. Anjouan Island.
34. *N. coquereli*. Mayotte Sunbird. Mayotte Island.
35. *N. venusta*. Pale-bellied Sunbird. Almost the whole Ethiopian region, from Senegal and Eritrea south to Natal, but not in lowland forests.
36. *N. fusca*. Dusky Sunbird. From the Karroo through southwestern Africa to Benguela.

#### NOTES:

The Seychelles sunbird provides a good link between the African subgenus *Cyanomitra* and the birds of the present group, which seem to have expanded first from Africa to the Orient, then returned to Africa via Madagascar. *N. souimanga*, in fact, differs from *N. jugularis rhizophorae*, from Hainan and Annam, only by its metallic green instead of grayish-olive mantle. The crown and underparts are completely similar. On the other hand, *N. humbloti* from Moheli and Great Comoro Islands has the dull mantle of *jugularis*, while the birds from the other two Comoros are much brighter and more saturated in both sexes; they still stem from *souimanga*, and their nearer African relatives are the birds of the widespread species *venusta*. The black abdomen of *comorensis* is no more significant of its relationships than is that of *asiatica*, or of the black-bellied subspecies of *jugularis*.

The white-bellied form of *venusta* in the northeast, *albiventris*, is linked to the yellow and orange-bellied forms (*fazoglensis*, *falkensteini*, *igneiventris*) through the very pale yellow *blicki*. The intensity of the color depends upon the habitat, turning white in dry districts (Friedmann, *U. S. Nat. Mus. Bull.*, 153, pp. 356-360, 1937). The white-bellied forms of the south and southwest, *talatala* and *oustaleti*, on the contrary, come into abrupt contact with the

yellow-bellied *falkensteini* and *kuanzae*.

The distribution of *oustaleti* remains confused on account of the mention by C. Grant and Mackworth-Praed (*Bull. B.O.C.*, LXIII, p. 70, 1943), of an immature specimen collected by A. M. Chapman at Mwenzo, Northern Rhodesia, the identification of which may not be absolutely certain. So far it had only been found in Angola. It does not seem that *talatala* really coexists anywhere with *falkensteini* (*nyassae*) in Nyasaland and Rhodesia. If this were the case, *N. talatala* would have to be considered a full species, with *oustaleti* as a subspecies. But it remains certain that sunbirds of this whole group are all very closely related.

*N. jugularis* has an extraordinarily wide range, but the conspecificity of all its forms cannot be doubted, even that of the black-bellied forms (*teijsmanni*, *clemenciae*, *keiensis* and *buruensis*) from the Moluccas, Djampea and Kalao. This was proved by the discovery of the black-bellied *N. j. idenburgi* Rand in New Guinea, where otherwise only yellow-bellied forms occur.

The bright orange-bellied green-crowned birds of the Lesser Sunda Islands, which coexist with yellow-bellied ones, must be considered as a separate species (*solaris*). They are probably the result of an earlier invasion. I prefer to consider *büttikoferi*, from Sumba, as a race of *jugularis* on account of its yellow underparts. *N. asiatica* is evidently also an off-shoot of *jugularis*, completely saturated with melanin.

*N. lotenia*, with its very long curved bill, and its dark highly metallic coloration, is difficult to place. I have, however, no doubt that it is the highly specialized product of an early invasion from Africa, and that *N. dussumieri* is its nearest, if still distant, relative.

*N. fusca* is a curious regressive desert species, but it appears to be near the *venusta* group, as shown by the female plumage pattern and the white lower abdomen of the male, as well as by its general shape.

The bird described as *Cinnyris picta* by Hachisuka from Basilan (*Proc. Biol. Soc. Washington*, 54, p. 52, 1941), seems to be a hybrid between *N. jugularis jugularis* and *N. sperata juliae* (See Zimmer and Mayr, *Auk*, 60, p. 259, 1943).

#### GROUP B.

In this group, birds vary from small to fairly large for the family. The tail is square, rounded or graduated. Males are always bright metallic green on the head, neck, mantle, throat. Underparts are gray, olive, or yellow, usually with a broad scarlet band across the chest, spreading to the greater part of the belly in two cases (*regia*, *rockefelleri*) and replaced by orange or olive yellow in two others (*loveridgei* and *vio-*

lacea). Females very plain, unmarked, gray to olive green, paler below than above.

All the males have pectoral tufts, which are absent in females. These sunbirds are purely African.

37. *N. chalybea*. Lesser Double-collared Sunbird. South Africa north to Angola and Lake Tanganyika.
38. *N. afra*. Greater Double-collared Sunbird. South and southeast Africa, to Angola, Lake Nyasa, Ruanda and Kivu Highlands, and Ruwenzori.
39. *N. mediocris*. East African Double-collared Sunbird. Highlands of Kenya and Tanganyika, south to Nyasaland.
40. *N. loveridgei*. Loveridge's Sunbird. Uluguru Mountains.
41. *N. preussi*. Mountain Double-collared Sunbird. High mountains of West Kenya, Ruwenzori, Kivu, Cameroon and Fernando Po.
42. *N. neergaardi*. Zambesi Double-collared Sunbird. Coast of southeast Africa, from northern Zululand to northern Portuguese East Africa.
43. *N. chloropygia*. Olive-bellied Double-collared Sunbird. West Africa and Fernando Po, to northern Angola, Uganda and southwestern Abyssinia.
44. *N. minulla*. Tiny Sunbird. Cameroon and Belgian Congo.
45. *N. regia*. Regal Sunbird. Ruwenzori and Kivu highlands, and Mt. Kungwe.
46. *N. rockefelleri*. Rockfeller's Sunbird. Mt. Kandashomwa, eastern Belgian Congo.
47. *N. violacea*. Wedge-tailed Sunbird. Western Cape Province to Little Namaqualand, South Africa.

#### NOTES:

All the species of this group with few exceptions resemble one another in such a way that it is difficult sometimes to distinguish them. A close study of the birds and of their geographical distribution enables one, however, to understand their relationships, which often have been confused.

*N. chalybea* is a moderate-sized bird with a comparatively narrow scarlet pectoral band and a very pale gray abdomen. The blue band on the upper breast and blue patch on the upper tail-coverts are reduced in size and of a steel blue; the latter is even absent in the race *intermedia* of Angola. They are southern birds of low or moderate altitudes. The recognizable races seem to be *chalybea*, *subalaris*, *zonaria*, *manoensis*, *gertrudis* and *intermedia*, but of some I have not been able to examine specimens.

*N. afra* is a bigger bird, with a longer, more graduated tail, a large bill, a wide scarlet band on the chest and a slightly

olive yellow darker shade on the abdomen. The blue of the chest-edging and the upper tail-coverts is more violet. Its green color is less golden. It is a bird of the lowlands or moderate elevation in south and southeast Africa (*afra*) and Angola (*ludovicensis*), with two mountain subspecies in central eastern Africa (*stuhmanni* and *graueri*). The last-named has a longer and more graduated tail than all the others. Quite independently, C. Grant and Mackworth-Praed (*Bull. B. O. C.*, LXIV, pp. 9, 10, 1943) have come to the same conclusions. Contrary to the opinion of several others, *N. chalybea intermedia* and *N. afra ludovicensis*, which occur together in Angola, are two very distinct birds.

*N. mediocris* occupies a central position, being smaller than *chalybea*, but larger than *preussi*. It has golden green upperparts, a steel blue band on the chest and upper tail-coverts, like *chalybea*, and strongly olive yellow lower breast and belly. It is a highland species of East Africa. Two subspecies, *mediocris* and *fülleborni*, occupy a large territory in E. Kenya and in Tanganyika. According to C. Grant and Mackworth-Praed (*Bull. B. O. C.*, LXIV, p. 10, 1943) *N. m. usambarica* (Grote) is a synonym of *mediocris*, and *N. m. moreaui* a synonym of *fülleborni*. I have been unable to examine specimens of *moreaui*, and have seen only one of *usambarica*, which does not appear to differ appreciably from a series of *mediocris*.

I am also in accord with Grant and Mackworth-Praed in considering the very peculiar *N. loveridgei* as a separate species. The scarlet chest-band is replaced in this bird by a small central patch, gradually merging with the intense olive yellow which extends all over the lower parts. *N. loveridgei* has been considered at times a form of *mediocris* or of *regia*, but it is much too different, in both sexes, to be included in either species. (See Grant and Mackworth-Praed, *ibid.*, pp. 10, 11). The female of *loveridgei* is peculiar in having a slightly metallic gloss on the upperparts.

*N. preussi*\* is still smaller than *mediocris*, to which it is similar, but very bright and with a dark olive brown abdomen. The band on the chest and the upper tail-coverts are violet blue and the scarlet extends far down on the breast. It is a mountain bird confined to high ground in East Africa (*kikuyensis*), Fernando Po, and Cameroon (*preussi*, *genderuensis*).

\* *Cinnyris reichenowi* Sharpe, *Ibis*, 1891, p. 444, is antedated by *Drepanorhynchus reichenowi* Fischer, *Journ. f. Orn.*, 1884, p. 56, as both species are here included in the genus *Nectarinia*. The next available name for this species is *Cinnyris preussi* Reichenow, *Journ. f. Orn.*, 1892, p. 190: Mt. Cameroon. The East African subspecies must now be called *N. preussi kikuyensis* Mearns, *Proc. U. S. Nat. Mus.*, XLVIII, p. 388, 1915: Escarpment Station, Kenya.



*N. neergaardi*, which I have not been able to examine, seems to be very similar to *N. preussi*, but larger with a still darker abdomen. A lowland bird of the Southeast coast, it can scarcely be a representative of the montane species.

*N. chloropygia* is a small, widespread species resembling *preussi*, but with no blue band on the breast nor blue patch on the upper tail-coverts. It lives at low and moderate altitudes. Its recognizable races seem to be *kempi*, *chloropygia*, *insularis*, *lühderi* and *orphogaster*. The status of *binechensis* still remains doubtful.

*N. minulla* closely resembles *chloropygia*, with which it coexists in Cameroon and the eastern part of the Belgian Congo. It is smaller and the scarlet chest-band is slightly mottled with metallic blue, this effect being produced by a narrow subterminal blue band in the feathers. It has white instead of gray under wing-coverts.

*N. regia* is a little more like *mediocris*. It has a long, graduated tail; its underparts are bright scarlet in the middle, widely golden yellow at the sides and olive yellow on the lower abdomen; under tail-coverts scarlet; chest-band and upper tail-coverts violet blue. It is a high altitude bird.

From the eastern Belgian Congo another bird, *N. rockefelleri*, was described by Chapin in 1932. It is very near *regia* but differs in having the whole breast scarlet without yellow borders, and has a longer bill. It seems strange that two distinct species of such similar appearance can live on the same mountain (Mt. Kandashomwa, west of the Ruzizi Valley); but until more is known about it we must list *rockefelleri* as a full species.

*N. violacea* is the most aberrant of the group. It is highly specialized in its long tail and orange-yellow breast, but regressive in its dull olive lower back and tail. However, it belongs distinctly in the present group, as the female plumage shows.

#### GROUP C.

These sunbirds vary from small, square-tailed forms to large ones with long central rectrices. Males have extremely brilliant metallic colors, ranging from golden green to shiny violet and coppery red, with a black or metallic lower breast and abdomen. Females are gray or olive above, paler below, not at all or only faintly marked underneath.

The males of three species, *habessinica*, *bouvieri*, *osea*, are tufted. Members of this group inhabit Africa, Arabia, Palestine and southern Syria.

48. *N. habessinica*. Shining Sunbird. Red Sea Province, Abyssinia, Somaliland, northeastern Uganda, and southwestern Arabia.

49. *N. bouvieri*. Bouvier's Sunbird. Savannas of Loango Coast, Cameroon, northern and southern Congo, base of Ruwenzori and Uganda.

50. *N. osea*. Orange-tufted Sunbird. Southern Syria, Palestine, Arabia, Chad Territory, Darfur, Lado district of the Sudan and the northern Belgian Congo.

51. *N. cuprea*. Coppery Sunbird. Savannas from Senegal to Abyssinia, south to the Congo, Angola and Nyasaland.

52. *N. tacazze*. Tacazze Sunbird. Highlands of Eritrea, Abyssinia, Kenya Colony and Kilimanjaro.

53. *N. bocagei*. Bocage's Sunbird. Highlands of Angola.

54. *N. purpureiventris*. Purple-breasted Sunbird. Ruwenzori and Kivu Mountains.

#### NOTES:

It is mostly by the similar plumage of the females that these seven species show their affinities. The males vary greatly in colors, as could be expected of such bright birds.

The resemblance in color of *N. cuprea* and *N. tacazze* is extremely striking, and their great difference in size, as well as the elongated central rectrices of the male *tacazze*, are the main distinctions between them.

*N. bocagei* seems to be a dull, regressive offshoot of *tacazze*, while *N. purpureiventris*, which tops the group, is one of the most elaborately beautiful species of the whole family.

#### GROUP D.

This is another group of small and large species, short or long-tailed, much like the preceding one, to which it is closely related. Males also have very bright metallic colors, but always of different shades of green and blue above. Abdomen black or metallic. The females of the short-tailed species differ from those of Group C in being darker above and more or less strongly mottled below. Those of the long-tailed forms gradually become paler and plainer.

Males are without pectoral tufts except in three extreme species (*coccinigaster*, *famosa*, *johnstoni*). The female of *johnstoni* is the only tufted one of the whole subgenus. All species are Ethiopian.

55. *N. shelleyi*. Black-bellied Double-colored Sunbird. Lower Zambesi Valley to northern Rhodesia.

56. *N. bifasciata*. Purple-banded Sunbird. Southern and eastern Africa, north to the Loango Coast, Lake Edward, East

Africa, Zanzibar and Pemba Islands, Abyssinia and Eritrea.

57. *N. coccinigaster*. Splendid Sunbird. From Senegal through West African savannas to northern Belgian Congo; also Gaboon.
58. *N. erythroceria*. Red-chested Sunbird. Upper Nile Valley to Uganda, the country around Lake Victoria, and Congo Valley west to Lukolela.
59. *N. pulchella*. Beautiful Sunbird. Senegal to northern Nigeria, Abyssinia, Eritrea, Kenya Colony, southern Somaliland and northern Tanganyika Territory.
60. *N. famosa*. Malachite Sunbird. East and South Africa from Abyssinia to Cape Province (highlands).
61. *N. johnstoni*.\* Scarlet-tufted Sunbird. Mountains of Kenya Colony, Kilimanjaro, Ruwenzori and northern Nyasaland.

#### NOTES:

This group includes some of the most beautiful sunbirds. *N. shelleyi*, a species restricted to a rather small territory, is evidently related to *bifasciata*, and to some extent also to *habessinica* and to *neergaardi*. It lacks, however, the yellow pectoral tufts of both those species, and the female is mottled below, showing a close affinity to *N. bifasciata*.

*N. bifasciata* is a widespread and highly variable species. The small western race *bifasciata* reaches Lake Tanganyika, and is replaced along the coast of East Africa, up to southern Kenya Colony, by the almost identical *microrhyncha*, which is also present on Zanzibar Island. In South Africa and on the highlands of East Africa and Abyssinia live four larger subspecies: *mariquensis*, *suahelica*, *osiris* and *hawkeri*. All these forms have a definite dark red band on the breast between a violet band and the black belly. In the drier parts of coastal Kenya Colony and southern Somaliland one finds two races: *tsavoensis* and *chalomelas*. Although closely related to those just mentioned, they differ considerably in the purer black of the lower breast and abdomen, and in the absence of the dark red band. They have a wide bright violet band above the black lower parts.

The local race of Pemba Island, *pembae*, still accentuates this characteristic. It is bluer above and in its coloration matches almost completely the Grand Comoro form *möbii*, of the Madagascan species *N. notata*, a very much larger bird.

\* *Nectarinia johnstoni salvadorii* (*N. salvadorii* Shelley Bull. B.O.C., XIII, p. 61, 1903. Kachere, Nyasaland) is preoccupied by *Nectarinia sericea salvadorii* (*Cinnurus salvadorii* Shelley, Moner. Sunbirds, p. 105, pl. 35, 1877, Jobi). I propose for it the new name: *Nectarinia johnstoni nyikensis*.

*N. coccinigaster*, one of the brightest species, suggests a glorified *N. bifasciata*. Females of both species are very similar.

The three other species of the group have elongated central rectrices, still fairly short in certain races of *erythroceria* and *pulchella*. I consider *congensis* as a subspecies of *erythroceria*, both sexes being generally similar. They have fairly long first primaries and no eclipse plumage.

The eastern and southern representatives of *N. pulchella* are *melanogaster*, *nectarinoides* and *erlangeri*. They differ mainly in their dull black instead of metallic green belly, the varying extent of yellow on the sides, and the length of the central rectrices. From the examination of good series, I have come to the conclusion that *melanogaster* and *nectarinoides* are probably conspecific, the latter representing a small, saturated form of *pulchella*, with short bill and tail. From all available information, I cannot find that the ranges of the two species really overlap. According to van Someren both have been found at Magadi, but this may have happened just at the limits of their respective habitats, where wandering birds might meet during the off-season in their search for flowering trees. It seems that *nectarinoides* is adapted to the semi-desert eastern country of southern Kenya Colony and northeastern Tanganyika Territory, while *melanogaster* prefers the less dry, open scrub and bush-velt to the west.

I agree with Grant and Mackworth-Praed (Bull. B.O.C., LXIV, p. 8, 1943) that *nectarinoides* is not so closely related to *erythroceria* as to *melanogaster*, but I do not think that it ought to be considered a valid species. It is true, however, that *nectarinoides* almost links the *pulchella* group with *erythroceria*, since its female approaches that of the latter species by its dark throat.

Grant and Praed are mistaken when they mention "tufts" in *pulchella*, *melanogaster* and *nectarinoides*. None of these sunbirds possesses any real pectoral tufts of erectile fluffy feathers. They merely have normal yellow feathers on the sides of the breast, which are few in number in *nectarinoides*. They are as completely devoid of pectoral tufts as *erythroceria*. The difference in the length of the first primary in *nectarinoides* and in *melanogaster* is proportionate to the size of the two birds; *erythroceria* and *congensis* have decidedly longer ones.

*N. famosa* is a much larger relative of *pulchella*, and *N. johnstoni* is a handsome high mountain form, in which the female is red-tufted like the male, a strange reappearance of a character found in some primitive species of the genus.

## GROUP E.

The birds of this last group are all large and very brightly colored. The males have either short, square tails or long rectrices. The short-tailed species are iridescent green above, the two long-tailed ones being coppery or bronze; the abdomen in all of them is black. The females differ from those of other groups in their yellow underparts streaked with dark olive gray. In two species (*superba* and *reichenowi*) these markings are faint; in the other four they are conspicuous. The female of *superba* is unusual in its orange under tail-coverts.

In only one species, *johannae*, the male has yellow pectoral tufts. These birds occur in Africa, Madagascar and the Comoro Islands.

62. *N. notata*. Angaladian Sunbird. Madagascar, Comoro Islands.
63. *N. johannae*. Johanna's Sunbird. West Africa from Sierra Leone to the Congo mouth, east to the Ituri district of the Belgian Congo.
64. *N. superba*. Superb Sunbird. West Africa from Sierra Leone to northern Angola and east to Uganda.
65. *N. kilimensis*. Bronzy Sunbird. Ituri highland, Uganda and Kenya Colony, south to Mashonaland and Angola.
66. *N. reichenowi*. Golden-winged Sunbird. Highlands of Kenya Colony and Uganda, south to Ngorongoro in Tanganyika Territory, west to the southern Kivu district.

## NOTES:

I have pointed out above the similiarity in color between the males of certain races of *N. notata* and *N. bifasciata*. On the other hand, females of *notata* resemble closely those of *N. johannae*, so that *notata* tends to link the two groups.

*N. superba*, with its gorgeous male and pale-bellied female, represents the extreme of a line of evolution, and is certainly close to *johannae*. These two species are the only ones of the subgenus *Nectarinia* to have a velvety dark red breast, suggestive of that found in the subgenus *Leptocoma*, particularly in some races of *N. sperata*.

Males of *N. kilimensis*, long-tailed and coppery green in color, are very different from those of the foregoing species, but the general similarity of the females shows their relationship.

The female of *N. reichenowi* resembles that of *kilimensis* in shape and color. The strongly curved bill of *reichenowi* is almost matched by that of *N. kilimensis arturi*. This evident proof of near relationship between the two species makes it impossible to admit generic distinction (*Drepanorhynchus*) for *reichenowi*. This wonderful

species, in which both sexes have the rectrices, primaries and secondaries bordered with golden yellow, represents the most specialized and elaborate form of the group, and perhaps of the whole genus.

III. GENUS *Neodrepanis*.

The small Madagascan sunbirds of this genus are remarkable in the large fleshy blue wattle around the eye of the breeding male and in the shape of the first primary. This feather is extremely long, scarcely shorter than the second, which equals the seventh in length, the third to fifth being the longest; and it is emarginate at the tip. The tail is extremely short and soft. The bill is very long and strongly curved, with very slight serrations on the lower mandible and none on the upper one.

In both species, which are closely related, there is an eclipse plumage in the males, which in breeding dress are dark metallic blue above and yellow below. Females and off-season males are olive green above, yellow mixed with olive brown below. On account of its form, size and color pattern, *Neodrepanis* seems clearly connected with *Nectarinia*, particularly the subgenus *Cyanomitra*. There are no pectoral tufts. The genus is confined to Madagascar.

1. *N. hypoxantha*. Slender-billed Wattled Sunbird. Highlands of central eastern Madagascar—probably extinct.
2. *N. corruscans*. Wattled Sunbird. Eastern Madagascar at moderate altitudes.

## NOTES:

F. Salomonsen has contributed an important paper on the sunbirds of this genus. (*L'Oiseau*, 1934, pp. 1-9, col. pl.).

IV. GENUS *Aethopyga*.

The sunbirds of this genus differ considerably from those of the three preceding genera in the structure of their tongue, which shows a flat terminal lobe between two semi-cylindrical ones. They possess that important characteristic in common with the following genus, *Arachnothera*, from which they differ, however, in other structural features. All species of *Aethopyga* are small. They have a rather short and curved bill, longer however than the head, and variable, with a distinctly ridged culmen. Nasal operculum bare. Wing rounded; the first primary short; third, fourth and fifth the longest. Tail rounded to much graduated; the central rectrices pointed in several species, very long in others. Males possess metallic colors, but they are never extensive, and are confined to the whole or portions of the head, neck, throat

VARIATIONS OF COLORS OF BREAST AND LOWER BACK IN MALES,  
*Aethopyga gouldiae*, *Ae. nipalensis* and *Ae. saturata*.

SPECIES AND SUBSPECIES	GEOGRAPHICAL DISTRIBUTION	COLOR OF BREAST				COLOR OF LOWER BACK	
		Yellow	Red Streaked Yellow	Red	Black	Yellow	Not Yellow
<b><i>Aethopyga gouldiae</i></b>							
<i>gouldiae</i>	E. Himalaya, W. Burma		I			I	
<i>isolata</i>	S. W. Burma	I				I	
<i>annamensis</i>	S. Indo-China	I					I
<i>harrietae</i> , }	E. Burma, N. Siam, N.			I		I	
<i>dabryi</i> }	Indo-China, S. C. W. China						
<b><i>Aethopyga nipalensis</i></b>							
<i>nipalensis</i> , }	E. Himalaya, Burma, W.		I			I	
<i>victoriae</i> , }	Yunnan, Tonking, Malay						
<i>australis</i> }	Peninsula						
<i>horsfieldi</i>	W. Himalaya	I*				I	
<i>blanci</i>	C. Laos		I				I
<i>ezrai</i>	S. C. Annam	I					I
<i>angkanensis</i>	N. W. Siam			I		I	
<b><i>Aethopyga saturata</i></b>							
<i>saturata</i> ,	Himalaya, N. Burma, W.				I	I†	
	Yunnan						
<i>sanguinipectus</i> , }	S. E. Burma, S. E. Yun-		I			I	
<i>wrayi</i> }	nan, N. Siam, N. C. and						
	W. Indo-China; Malay						
	Peninsula						
<i>anomala</i>	Peninsular Siam		I				I
<i>johnsi</i>	S. Annam			I		I	

\* Some specimens show a few faint red streaks.  
† Many specimens have a small yellow patch, others none.

and tail, and, exceptionally, to the wing-coverts. In the most primitive species, *boltoni*, there are only faint traces of metallic sheen on the crown and tail. The sides of the head are never metallic. There is always a good deal of silky red or olive yellow in the plumage. The lower back is usually bright yellow; but this patch disappears in certain subspecies of *saturata*, *nipalensis*, and *gouldiae*, and in *flagrans*. A very important and characteristic feature of the genus is the long, fluffy feathers of the sides of the lower back. There are no pectoral tufts. Females are dull olive above, with a grayish hood in several species.

The species of *Aethopyga* are found from India to central and southeastern China, the Philippines, Sumatra, Java, Borneo, Sanghir Island and Celebes.

1. *Ae. boltoni*. Mindanao Sunbird. Mindanao.
2. *Ae. flagrans*. Flaming Sunbird. Northern Philippines (Luzon, Negros, Panay, etc.).
3. *Ae. pulcherrima*. Sharpe's Sunbird. The Philippines.

4. *Ae. duyvenbodei*. Duyvenbode's Sunbird. Sanghir Island.
5. *Ae. shelleyi*. Lovely Sunbird. Palawan and the Philippines.
6. *Ae. gouldiae*. Mrs. Gould's Sunbird. The Himalayas, Assam, Burma, Siam, central and southern China, Indo-China.
7. *Ae. nipalensis*. Yellow-bellied Sunbird. East Himalaya, Assam, Burma, Siam, Indo-China, southern China, Malay Peninsula (mountains).
8. *Ae. eximia*. Kuhl's Sunbird. Java.
9. *Ae. christinae*. Sharp-tailed Sunbird. Southeastern China, eastern Indo-China, Hainan.
10. *Ae. saturata*. Black-breasted Sunbird. The Himalayas, Burma, Siam, Yunnan, Indo-China, Malay Peninsula.
11. *Ae. siparaja*. Yellow-backed Sunbird. From India to southern China, Siam, Indo-China, Philippines, Malay Peninsula, Sumatra, Java, Borneo, Celebes.
12. *Ae. mystacalis*. Scarlet Sunbird. Malay Peninsula, Sumatra, Borneo, Java.

13. *Ae. ignicauda*. Fire-tailed Sunbird.  
Himalaya, Assam, Burma, Yunnan.

## NOTES:

The simplest forms of *Aethopyga* are found in the Philippines. *Ae. boltoni* has a graduated tail and a yellow back, but the metallic sheen on the dark gray crown is hardly noticeable.

*Ae. flagrans*, rightly ascribed by Oustalet to *Aethopyga*, has since been wrongly placed in the genus *Cinnyris* (*Nectarinia*) by several authors. It is difficult to account for such a mistake, as it has all the important characteristics of *Aethopyga*, particularly the texture of the plumage. The alleged resemblance to *Nectarinia jugularis aurora* is entirely superficial. *Ae. flagrans* has a metallic crown, chin and tail, but lacks the yellow patch on the lower back and has a rounded tail.

*Ae. pulcherrima* has broad metallic borders to all the wing-feathers except the primaries, a feature which it shares with *Ae. duyvenbodei*, and a short, almost square tail. *Ae. duyvenbodei*, however, is closely allied to *Ae. shelleyi* in its general color pattern.

The small Philippine forms usually referred to *bella* are conspecific with *Ae. shelleyi* from Palawan, which is merely larger and more highly colored, and has a longer tail.

*Ae. gouldiae* is certainly the continental representative of the preceding species, larger and brighter, with a very long tail. *Ae. dabryi* and *Ae. harrietae*, from China and northern Indo-China, which have red breasts, are nothing but subspecies of *gouldiae*. *Ae. g. annamensis*, from South Annam and South Laos, lacks the yellow patch on the lower back. Both *Ae. gouldiae* and *Ae. shelleyi* have very small bills.

*Ae. nipalensis* also has two Indo-Chinese races with no yellow patch on the lower back (*ezrai* and *blanci*), both very rare and found on high mountains. On the isolated mountain of Doi Angka, in Siam, lives the peculiar race *angkanensis* with an unstreaked grenadine red chest. *Ae. n. ezrai* and *horsfieldi* have it plain yellow, while all other forms have a yellow chest streaked with red to a greater or lesser degree. The amount of maroon red on the upper back varies considerably.

*Ae. eximia* and *Ae. christinae* show a certain agreement in colors.

*Ae. saturata* includes *Ae. sanguinipectus* and its allies as subspecies. Typical *saturata* often lacks the yellow patch on the lower back, or has it much reduced, while *anomala* from peninsular Siam has none. The form *johnsi*, isolated on the Langbian highlands of Southern Annam, is the most distinct of all the subspecies of *saturata*, having

even been considered often as a full species. It is small in size, with a comparatively short tail; the black pectoral band is almost absent, and the whole chest is grenadine red faintly streaked with yellow.

In the species *gouldiae*, *nipalensis* and *saturata*, isolation in highland areas favors variation in the color of breast and back. Yet when two or more of the species live together in the same locality they do not exhibit any parallelism in these respects. Curiously enough, when males lack the yellow rump-patch, females of the same race appear to retain it (*Ae. saturata anomala*, *Ae. nipalensis blanci*, *Ae. gouldiae annamensis*).

*Ae. siparaja* is a common and widespread lowland species found from southern and western India (*vigorsi*) throughout Burma, South China, Siam, Indo-China and the Malay countries, to the Philippines (*magnifica*) and Celebes (*flavostriata*).

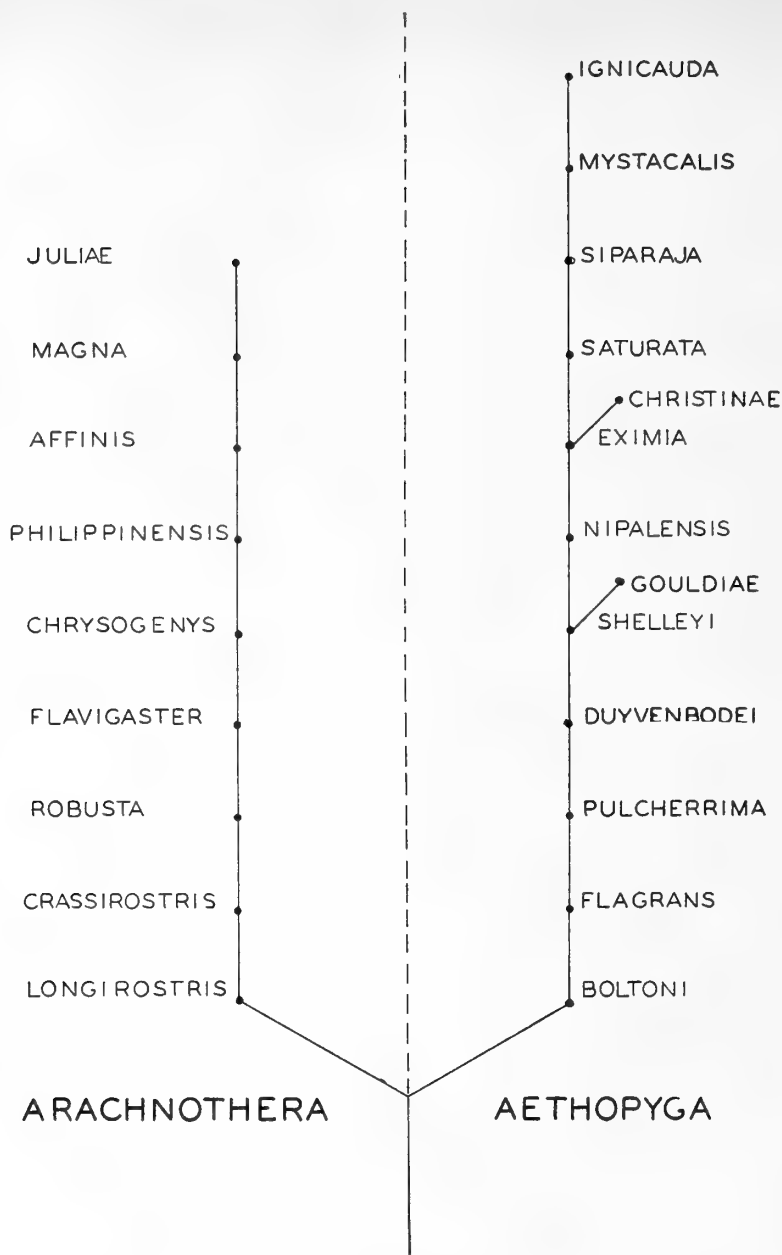
*Ae. mystacalis* and *Ae. temmincki* are conspecific in spite of the difference in the color of their long rectrices (glossy violet and vermilion scarlet). *Ae. ignicauda*, remarkable for its long vermilion red tail, is the only species of the genus to have an eclipse plumage.

V. GENUS *Arachnothera*.

The birds of this genus differ considerably from all other sunbirds, but they are nearest to *Aethopyga*. They are large and coarse with a massive body, a short, rounded tail; they have a long and very strong bill, short tarsi but powerful toes and sharp nails. Nostrils naked, and wings as in *Aethopyga*. They show no metallic colors in the plumage, which is olive, gray, and yellow—brown in one case. Three species possess pectoral tufts in the males. Their tongue is similar to that of *Aethopyga*, and they also have long, fluffy feathers on the sides of the lower back. In their diet, these birds are much more insectivorous, less nectar-sucking, than the other sunbirds.

*Arachnothera* is an Indo-Malayan genus. Two species extend to India, Siam, Burma and Indo-China, while others barely reach the extreme south of some of these countries. It is also represented in the Philippines, but the Malaysian region is its stronghold.

1. *A. longirostris*. Little Spider-hunter. India, Burma, Yunnan, Siam, Indo-China, Malay Peninsula, Sumatra and neighboring islands, Borneo, Java, Palawan, Philippines.
2. *A. crassirostris*. Thick-billed Spider-hunter. Malay Peninsula, Sumatra, Borneo.



TEXT-FIG. 14. Species of the Genera *Arachnothera* and *Aethopyga*.

3. *A. robusta*. Long-billed Spider-hunter. Malay Peninsula, Sumatra, Borneo, Java.
4. *A. flavigaster*. Great Yellow-eared Spider-hunter. Cochin-China, Malay Peninsula, Sumatra, Borneo.
5. *A. chrysogenys*. Yellow-eared Spider-hunter. Tenasserim, Peninsular Siam, Cochin-China, Malay Peninsula, Su-

- matra and neighboring islands, Borneo, Java.
6. *A. philippinensis*. Naked-faced Spider-hunter. Philippines.
7. *A. affinis*. Gray-breasted Spider-hunter. Tenasserim, Peninsular Siam, Cochin-China, Malay Peninsula, Sumatra, Borneo, Java, Bali.
8. *A. magna*. Streaked Spider-hunter.

Himalaya, Assam, Borneo, Yunnan, Siam, Indo-China, Malay Peninsula.

9. *A. juliae*. Whitehead's Spider-Hunter. Borneo (mountains).

#### NOTES:

The first three species are the nearest to the other sunbirds. The males have orange pectoral tufts, and the feathers on the sides of the lower back are very long and fluffy. The species *longirostris*, the smallest, with a slim but very long bill, is the most widespread; *diluta* from Palawan and *flammiifera* from the Philippines are among its subspecies.

*A. flavigaster*, *chrysogenys* and *philippinensis* are well differentiated species.

*A. affinis*, *magna* and *juliae* are certainly related and very similar in shape and size, but constitute separate species, although *juliae* is the representative of *magna* on the high mountains of Borneo and belongs to the same superspecies. But it is too different in its color pattern (brown streaked with white, and golden yellow on under tail-coverts) to be considered a subspecies of *magna*. *A. affinis* coexists with *magna* in the Malay Peninsula and Tenasserim.

#### ECLIPSE PLUMAGE.

In a certain number of species of sunbirds, males have a double annual molt and take on a dull plumage resembling that of the females, keeping it for a period of several months after the breeding season. The presence or absence of this eclipse plumage seems to have little systematic significance, since it varies in closely allied forms, even in different subspecies of the same species. It appears that birds from the dry and colder parts, where sharply contrasted seasons alternate, often possess an eclipse plumage. Those living near the equator in tropical forests seldom show it. But there are certainly many exceptions to the rule.

Comparatively little is known on the subject. The study of museum collections is of help only in the case where it is certain that males are molting from bright into dull dress. The occurrence in a series of many males in transition plumage may only mean that a number of young birds, just assuming their adult dress, have been secured. I myself have been almost misled by a large series of *Aethopyga gouldiae harrietae*, collected in Laos during the months of November and December, 1938. I had good reason to believe that our very numerous males in transition plumage meant that this form had an eclipse dress. But the observation of captive specimens living in my tropical conservatory at

Clères, proved that it had none. Careful and prolonged observation of live birds at liberty or in captivity, under suitable conditions, can make certain that a seasonal eclipse plumage is assumed by a given form. We still are in doubt as to many species and subspecies. As an encouragement for further investigations, I am giving here the list of records which are definitely established, by my personal observations and by those of reliable naturalists.

#### 1. SPECIES OF SUNBIRDS IN WHICH THE MALE HAS AN ECLIPSE PLUMAGE.

*Anthreptes platara*

*Nectarinia amethystina amethystina*

" *lotenia*

" *jugularis*

" (Indo-Malayan races)

" *asiatica*

" *souimanga*

" ? *venusta kuanzae*\*

" *fusca*

" *afra* (southern races)

" *chalybea*

" *cuprea*

" *pulchella*

" *famosa*

" *reichenowii*

*Neodrepanis hypoxantha*

" *coruscans*

*Aethopyga ignicauda*

#### II. SPECIES OF SUNBIRDS HAVING NO ECLIPSE PLUMAGE.

All *Anthreptes* except *platara*

All *Nectarinia* of the subgenera *Cyanomitra*, *Chalcomitra* (except *N. a. amethystina*), *Leptocoma*  
*N. venusta* (except *kuanzae*)  
*N. mediocris*  
*N. chloropygia*  
*N. minulla*  
*N. violacea*  
*N. tacazze*  
*N. bifasciata*  
*N. erythroceria*  
*N. notata*  
*N. coccinigaster*  
*N. johannae*  
*N. superba*  
*N. kilimensis*

All *Aethopyga* (except *Ae. ignicauda*)

All *Arachnothera*

The occurrence of an eclipse plumage in all other species remains unrecorded.

\* In a large series in the American Museum, collected by Ansonje in July and August, not a single male is in breeding plumage.

† The eclipse plumage of this species is partial: the male retains its yellow wings and tail, but the coppery lustre of its head, neck, upper back and breast is replaced by a dull black.



## ALPHABETICAL LIST OF GENERIC NAMES.

In **bold face**, valid genera; in SMALL CAPITALS, subgenera; in *italics*, synonyms.

*Adelinus* Bonaparte, 1854. (*N. verreauxi*) = *Nectarinia*.

*Aethocinnyris* A. Roberts, 1922. (*N. afra*) = *Nectarinia*.

**Aethopyga** Cabanis, 1850. (*Ae. siparaja*).

*Aidemonia* Reichenbach, 1854. (*N. cuprea*) = *Nectarinia*.

*Anabathmis* Reichenow, 1905. (*N. reichenbachii*) = *Nectarinia*.

*Anagaladiana* Reichenbach, 1854. (*N. notata*) = *Nectarinia*.

*Anthobaphes* Cabanis, 1850. (*N. violacea*) = *Nectarinia*.

*Anthodiaeta* Cabanis, 1850. (*A. collaris*) = *Anthreptes*.

*Anthophagana* Strand, 1928. (*N. olivacea*) = *Nectarinia*.

*Anthophagus* Jennings, 1829. (*N. olivacea*) = *Nectarinia*.

*Anthothreptes* Cabanis, 1850. (*A. malacensis*) = *Anthreptes*.

**Anthreptes** Swainson, 1837. (*A. malacensis*).

*Arachnecethra* Cabanis, 1850. (*N. lotenia*) = *Nectarinia*.

*Arachnocestra* Reichenbach, 1854. (*A. crassirostris*) = *Arachnothera*.

*Arachnophila* Salvadori, 1874. (*A. simplex*) = *Anthreptes*.

*Arachnoraphis* Reichenbach, 1854. (*A. flavigaster*) = *Arachnothera*.

**Arachnothera** Temminck, 1826. (*A. chrysogenys*).

*Bapthorax* A. Roberts, 1922. (*N. senegalensis gutturalis*) = *Nectarinia*.

*Carmelita* Reichenbach, 1854. (*N. fuliginosa*) = *Nectarinia*.

CHALCOMITRA Reichenbach, 1854. (*N. amethystina*) subgenus of *Nectarinia*.

*Chalcoparia* Cabanis, 1850. (*A. phaenicotis*) = *Anthreptes*.

*Chalcostetha* Cabanis, 1850. (*N. chalcostetha*) = *Nectarinia*.

*Chromotophora* Reichenbach, 1854. (*N. superba*) = *Nectarinia*.

*Cinnyris* Cuvier, 1817. (*N. superba*) = *Nectarinia*.

*Cinnyricinclus* Lesson, 1840. (*A. longuemarei*) = *Anthreptes*.

CYANOMITRA Reichenbach, 1854. (*N. verticalis cyanocephala*) subgenus of *Nectarinia*.

*Cyrstostomus* Cabanis, 1850. (*N. jugularis*) = *Nectarinia*.

*Drepanorhynchus* Fischer and Reichenow, 1854. (*N. reichenowi*) = *Nectarinia*.

*Dreptes* Reichenow, 1914. (*N. thomensis*) = *Nectarinia*.

*Duyvena* Mathews, 1925. (*Ae. duyvenbodei*) = *Aethopyga*.

*Eleocerthia* Reichenbach, 1858. (*N. verreauxi*) = *Nectarinia*.

*Eremicinnyris* A. Roberts, 1922. (*N. fusca*) = *Nectarinia*.

*Euchoridia* Reichenbach, 1854. (*A. rectirostris*) = *Anthreptes*.

*Eucinnyris* A. Roberts, 1922. (*N. venusta talatala*) = *Nectarinia*.

*Eudrepanis* Sharpe, 1877. (*Ae. pulcherrima*) = *Aethopyga*.

*Gunningia* A. Roberts, 1922. (*A. reichenowi*) = *Anthreptes*.

*Haagneria* A. Roberts, 1925. (*N. olivacea*) = *Nectarinia*.

*Hedydipna* Cabanis, 1850. (*A. platara*) = *Anthreptes*.

*Helionympha* Oberholser, 1905. (*N. pulchella nectarinioides*) = *Nectarinia*.

*Hermotimia* Reichenbach, 1854. (*N. sericea*) = *Nectarinia*.

*Hypogramma* Reichenbach, 1854. (*N. hypogrammica*) = *Nectarinia*.

*Lamprothreptes* A. Roberts, 1922. (*A. longuemarei*) = *Anthreptes*.

LEPTOCOMA Cabanis, 1850. (*N. sperata braziliiana*) subgenus of *Nectarinia*.

*Leucochloridia* Reichenbach, 1858. (*N. verticalis*) = *Nectarinia*.

*Mangusia* Bonaparte, 1854. (*A. rectirostris*) = *Anthreptes*.

*Maricornis* A. Roberts, 1922. (*N. bifasciata mariquensis*) = *Nectarinia*.

*Microcinnyris* A. Roberts, 1922. (*N. chalybea*) = *Nectarinia*.

**Nectarinia** Illiger, 1811. (*N. famosa*).

*Nectarophila* Reichenbach, 1854. (*N. sperata braziliiana*) = *Nectarinia*.

**Neodrepanis** Sharpe, 1875. (*N. coruscans*).

*Notiocinnyris* A. Roberts, 1922. (*N. afra*) = *Nectarinia*.

*Panaeola* Cabanis, 1850. (*N. pulchella*) = *Nectarinia*.

*Platydidpna* Cabanis, 1850. (*A. platara*) = *Anthreptes*.

*Sclaterornis* A. Roberts, 1922. (*N. kilimensis arturi*) = *Nectarinia*.

*Shelleyia* A. Roberts, 1922. (*N. shelleyi*) = *Nectarinia*.

*Tephrolaema* Heine, 1860. (*A. rectirostris tephrolaema*) = *Anthreptes*.

*Urodrepanis* Shelley, 1876. (*A. christinae*) = *Aethopyga*.



## 5.

Two New Species of Fishes (Gymnotidae, Loricariidae)  
from Caripito, Venezuela.<sup>1</sup>

LEONARD P. SCHULTZ

Curator of Fishes, United States National Museum.

(Plate I; Text-figures 1-2).

[This is a contribution from the Forty-third or Venezuelan Expedition of the Department of Tropical Research of the New York Zoological Society made under the direction of Dr. William Beebe. The expedition was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela. For maps and ecological data, see *Zoologica*, Vol. XXVIII, No. 9, pp. 53-59, 1943.]

Dr. William Beebe, Director, Department of Tropical Research, New York Zoological Society, kindly loaned to me for study his collections made during 1942 in the region of Caripito, Venezuela, and I take this opportunity to express my thanks to him for the privilege of studying these specimens.

Among this interesting lot of fishes I found what I consider to be two new species. The first one described belongs to the family Gymnotidae, and to the not well known genus *Hypopomus* Gill. The second species belongs to the family Loricariidae and was received too late to include in my recent publication entitled "The Catfishes of Venezuela, with descriptions of thirty-eight new forms," *Proceedings of the United States National Museum*, vol. 94, pp. 173-338, figures 1-5, plates 1-14, 1944.

No doubt when more extensive collecting is done in the Caripito region of Venezuela additional undescribed species of fishes will be found.

## Family Gymnotidae.

Genus *Hypopomus* Gill.

*Hypopomus* Gill, *Proc. Acad. Nat. Sci. Phila.*, p. 152, 1864. Genotype: *Rhamphichthys mulleri* (Kaup).

After examining the material in the national collections along with 4 specimens

collected by Dr. William Beebe at Caripito, Venezuela, and comparing these with figures and descriptions of the already described species, considerable doubt must be cast on the identifications made by Ellis in his review of the family Gymnotidae and by Eigenmann in his British Guiana fishes, since both accounts are identical with but few exceptions. The specimens from Caripito have a very bluntly rounded snout and shorter head and the pore above the posterior nostril differs in position when compared with forms from other localities. Unfortunately, Kaup did not show the position of that pore in reference to the posterior nostril, but his measurements of, and his figure of, *artedi* indicate that this species has a pointed snout with the rear margin of the eye behind the middle of the length from snout to occiput, while in other forms it is an equal distance as shown in figures and in the specimens before me. Steindachner's figure of *brevirostris* fortunately shows the position of the pores in reference to the posterior nostril and these are the same as in the specimens that I am referring to *occidentalis* Regan from Panama and the Maracaibo Basin, but the species must be different since *brevirostris* has 259 or 260 anal rays instead of fewer than 240 in the other species. Because of the above differences, it appears probable that the specimens from Caripito represent an undescribed species, while those from the Maracaibo Basin are so close to those from Panama that I identify them as the same form. Measurements made on available specimens are recorded in Table I.

KEY TO THE SPECIES OF *Hypopomus* GILL.

- 1a. Anal rays about 259 or 260; the pore above the posterior nostril (see Text-figs. 1 and 2) lies behind a vertical line through the rear edge of the posterior nostril and this pore is more remote from nostril than nostril is from the edge of the eye; tail behind the anal fin

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rounded, tapering to a point and length of tail is contained about 4 times in the total length; distance from posterior nostril to eye contained about 10 to 15 times in snout to occiput; rear margin of eye near middle of length from tip of snout to occiput. (Río Guaporé).....

*Hypopomus brevirostris*  
(Steindachner)

1b. Anal rays fewer than 240, usually from 204 to 238.

2a. Rear margin of eye at least one-half to an eye diameter behind middle of length of distance from snout to occiput; snout contained  $2\frac{1}{2}$  to 3 times in the head and about  $1\frac{2}{3}$  in postorbital length of head; distance from posterior nostril to eye contained about 15 times in length from snout to occiput; pore above the posterior nostril lies behind a vertical line through rear edge of nostril. (Río Mona, French Guiana).....

*Hypopomus artedi* (Kaup)<sup>2</sup>

2b. Rear margin of eye midway between tip of snout and occiput; snout contained more than 2 times in postorbital length of head.

3a. Distance from posterior nostril to eye contained from 9 to 14 times in length from snout to occiput; the pore above the posterior nostril lies behind a vertical line through rear of nostril or this line bisects the pore (Text-fig. 2), the latter is separated from the nasal opening by an isthmus of skin; tail behind anal compressed and ending rather abruptly, not gradually tapering to a rounded point and contained about 5 to 6 times in the total length; snout  $2\frac{1}{5}$  to  $2\frac{1}{3}$  into postorbital length of head. Río Condoto; Panama; Maracaibo Basin).....

*Hypopomus occidentalis* Regan.

3b. Distance from posterior nostril to eye contained about 25 to 32 times in distance from snout to occiput; the pore above posterior nostril lies close to margin of that nostril and is bisected by a line through middle of posterior nostril or the pore is just in front of this line (Text-fig. 1); snout very bluntly rounded,  $2\frac{1}{2}$  to  $2\frac{4}{5}$  times in postorbital length of head; tail very little compressed, tapering to a point and contained about  $5\frac{1}{3}$  to 6 times in total length. (Caripito, Venezuela). *Hypopomus beebei* new species.

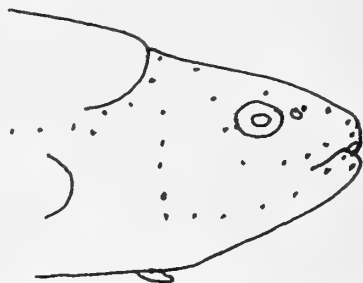
***Hypopomus beebei*, new species.**

Text-fig. 1; Plate 1, Fig. 4.

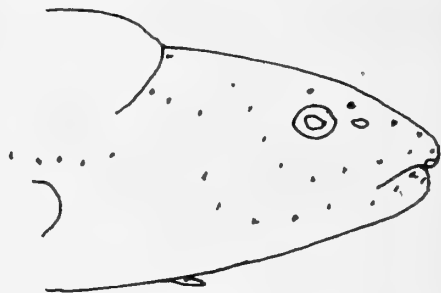
**Holotype:** U.S.N.M. No. 120753, a specimen, 136 mm. in total length and 112 mm. from snout tip to end of anal fin, collected by Dr. William Beebe at Caripito, Venezuela, during 1942.

**Paratypes:** Three specimens, 129 and 150 mm., the other specimen with tail broken off, taken along with the holotype and bearing same data (Cat. No. 30,040 in the collections of the Department of Tropical Research, New York Zoological Society).

**Description:** The holotype and 2 paratypes were measured, and these data, along with that recorded for other species, are presented in Table I.



TEXT-FIG. 1. Arrangement of pores on head of *Hypopomus beebei*.



TEXT-FIG. 2. Arrangement of pores on head of *Hypopomus occidentalis*.

Body compressed, tail slightly compressed and tapering to a point; head bluntly rounded; snout short, about equal to interorbital space, contained about  $4\frac{1}{5}$  times in head; jaws without teeth; length of pectoral fin 2 in head; lateral line straight, the 3 rows of scales below and about 4 rows above enlarged; scales along back and ventrally on body much smaller in size; head a trifle longer than greatest depth; origin of anal fin about opposite tips of pectorals; anal papilla present, its base under middle of opercle or a vertical line

<sup>2</sup> *Rhamphichthys mulleri* Kaup is referred to this species as a synonym. I have examined a specimen of *artedi* (I. U. No. 12620) kindly loaned by Dr. J. L. Kask, California Academy of Sciences, and refer it to this species.

TABLE I. Counts and Measurements Made on Species of *Hypopomus*, Expressed in Hundredths of the Length from Snout Tip to End of Anal Fin.

Characters	<div>beebeioccidentalisartedi brevirostris</div>						
	Holo-type	Para-type	Para-type	Maracaibo Basin	after Kaup	after Steindachner's figure	
Length to end of anal fin in millimeters...	112.	106.	124.	100.	137.	244.	252.
Length of anal fin base.....	83.0	84.0	83.9	85.0	81.7	.....	86.5
Length of head.....	12.1	12.3	11.7	13.1	12.4	13.5	11.7
Length of snout .....	3.21	3.11	3.06	4.0	3.87	5.12	2.78
Greatest depth .....	11.06	11.8	9.68	12.0	13.1	9.30	9.33
Width of interorbital space.....	3.03	3.30	3.14	3.00	2.72	.....	.....
Postorbital length of head.....	8.48	8.20	8.14	8.30	8.03	7.78	7.34
Snout to occiput.....	8.57	8.49	8.06	10.0	9.20	9.02	7.74
Diameter of eye.....	1.25	1.42	1.29	1.50	1.24	0.98	1.59
Distance from anterior to posterior nostril.	2.23	2.08	2.26	2.70	2.12	.....	1.90
Distance from eye to posterior nostril....	0.28	0.27	0.32	0.80	0.88	.....	0.56
Width of gill opening.....	2.41	2.73	2.58	2.70	3.22	.....	2.85
Snout to anus.....	8.48	9.34	8.14	9.50	8.61	7.10	8.92
Snout to anal origin.....	17.4	16.6	16.1	16.2	16.8	20.7	15.5
Anus to anal origin.....	9.64	7.83	8.39	7.50	8.39	.....	7.54
Snout to pectoral insertion.....	11.2	11.3	11.3	12.5	12.1	.....	11.7
Longest ray of pectoral fin.....	5.35	5.47	.....	6.20	5.84	5.29	5.36
Longest ray of anal fin.....	4.02	.....	.....	5.00	4.60	.....	3.77
Length of tail beyond anal fin.....	21.0	22.3	20.1	20.5	25.1	20.9	32.9
Width of head at eyes.....	4.46	5.19	4.92	4.30	3.87	.....	.....
Number of anal rays.....	214	228	217	204	223	220 or 223	259 or 260

through occiput passes through base of anal papilla; lower jaw very slightly shorter than upper; mouth terminal, small; cephalic canals and pores prominent; mucus pores numerous on head; gill opening extending a little above and below pectoral fin base and more or less enclosing it, except posteriorly; margin of eye not free; eye small, a little over two times in the interorbital space; interorbital space convex, about 3 times in distance from snout tip to occiput; fontanel present from between eyes to occiput.

*Color:* Body light brownish in alcohol with 17 narrow dark brown bars across sides to end of anal fin; sometimes an incomplete or broken bar occurs between most or all the nearly complete bars; pectoral fins and anal fin with numerous dark brown pigment specks; tail beyond anal fin with about 3 more brown bars more or less obscure or absent.

Named *beebei* in honor of Dr. William Beebe, collector of this new species, who so kindly loaned to me his fish specimens from Caripito, Venezuela.

Family *Loricariidae*.

*Corymbophanes venezuelae*, new species.

Text-fig. 2; Plate 1, Figs. 1-3.

*Holotype:* U.S.N.M., No. 120752, a speci-

men 72.5 mm. in standard length, 94.5 mm. total length, collected by Dr. William Beebe in the Río Caripe, Caripito, Venezuela, during 1942.

*Paratype:* A specimen 32.5 mm. in standard length, 45 mm. total length, collected with the holotype and bearing same data (Cat. No. 30064, in the collections of the Department of Tropical Research, New York Zoological Society).

*Description:* Detailed measurements were made on the holotype and paratype and these data, expressed in hundredths of the standard length, are recorded in Table II, along with comparative data taken from the photographs of *Corymbophanes andersoni* Eigenmann.

The following counts were made, respectively, for holotype and paratype: Dorsal rays I, 10; I, 9; anal rays ii, 4; ii, 5; pelvic rays I, 5-I, 5; pectoral rays I, 6-I, 6; I, 6-I, 6; branched caudal fin rays 14; 14; series of scutes along lower sides 24; 24; pores in lateral line 25; 25; plates in front of dorsal fin 4-3; 3-3; scutes between anal and caudal fins 11; 11; spinuels on preopercle 7 to 11; 2 hooked spines on interopercle.

Head depressed, body depressed forward, caudal peduncle a little compressed, triangular in cross section; rami of jaws long, the

TABLE II. Measurements, Expressed in Hundredths of the Standard Length, for Two Species of *Corymbophanes* Eigenmann.

Characters	<i>andersoni</i>	<i>venezuelae</i>	
	From figures of type	Holotype	Paratype
Standard lengths in millimeters.....	86.	72.5	32.5
Width across base of pectorals.....	30.0	37.2	32.9
Greatest depth .....	20.4	18.6	18.2
Snout .....	19.6	24.3	21.8
Interorbital space .....	11.7	10.3	12.3
Diameter of the eye.....	3.83	4.96	6.46
Length of ramus of lower jaw.....	8.33	11.0	10.8
Distance from nostrils to snout tip.....	13.8	18.2	14.8
Distance from nostrils to eye.....	4.58	4.14	3.39
Greatest width of lower lip.....	7.92	7.86	7.08
Tip of snout to gill opening.....	.....	27.6	25.6
Tip of snout to occiput.....	25.8	35.2	34.2
Distance from eye to rear of temporal plate.....	8.08	9.66	9.85
Length of caudal peduncle.....	28.8	24.1	27.1
Least depth of caudal peduncle.....	11.2	13.8	14.8
Length of first dorsal ray.....	19.7	20.7	26.2
Length of last dorsal ray.....	10.4	14.1	14.2
Length of pectoral spine.....	24.6	26.6	26.7
Length of upper caudal ray.....	26.7	21.4	28.6
Length of lower caudal ray.....	29.2	27.9	31.7
Length of longest anal ray.....	7.92	9.10	6.16
Snout to dorsal origin.....	45.0	46.9	44.6
Snout to anal origin.....	64.7	71.7	71.0
Anus to anal origin.....	.....	9.38	10.2
Length of base of dorsal fin.....	19.6	26.2	24.9

ramus of the lower jaw contained 0.9 and 1.0 times in the interorbital space; head (to end of temporal plate) 2.8 and 2.7, depth 5.5, both in standard length; eye  $3\frac{1}{2}$  and  $4\frac{1}{2}$  in snout; eye  $4\frac{1}{2}$  and 6 in head to end of opercle and 5 and  $7\frac{1}{2}$  to end of temporal plate; eye 1.5 and 1.7 in interorbital space; lips of oral disk papillate, the papillae larger near margin of upper lip; length of free portion of maxillary barbel about  $\frac{2}{3}$  eye diameter; ramus of upper jaw not quite as long as ramus of lower jaw; both jaws with numerous very fine teeth with bifid tips, the inner lobe longest; ventral surface naked from anal fin region forward; anterior portion of head from just in front of nostrils and eyes naked, but with small, firm, embedded nodules; this naked area extends along sides of head to include interopercle and base of opercle; interorbital space slightly convex and free of prickles except a few over orbit, top of head to occiput also free of prickles; predorsal scutes in 3 or 4 pairs; dorsal surface of head evenly convex; no ridges or grooves on the head; none of the plates is keeled on the head or sides of body; each side of dorsal fin base naked; adipose fin completely lacking and no ridge where this fin might be expected; origin of dorsal fin an eye diameter in front of a vertical line through pelvic insertion; insertion of pelvics a trifle closer to tip of snout than midcaudal fin base; first two or three branched rays of dorsal fin longest; caudal fin a trifle concave; lower lobe long-

est; margin of dorsal fin a little rounded; third branched ray of pelvics longest; a vertical line through origin of anal fin is a little closer to base of last dorsal ray than to its tip; pectoral fins reach to or just past pelvic base and pelvic fins just past anal fin base; the opercle and interopercle are separately movable, the latter with two hooked short spines, their bases covered by thick skin; there are from 7 to 11 small spinules on the opercle.

*Color:* Caudal and dorsal fins barred; general coloration in alcohol brownish. No black spots along base of dorsal fin or on upper or lower surfaces of the body.

*Remarks:* This new species, *Corymbophanes venezuelae*, is a *Chaetostoma* lacking an adipose fin. If certain other characters, when compared with various species referred to *Chaetostoma*, were not different, too, I would be inclined to refer it to that genus since certain species, as *Chaetostoma anomala*, occasionally lack an adipose fin. The chief difference between these genera, besides the adipose fin, is in the degree of nakedness of the snout and the backward extension of this naked area to include the interopercle and most of the opercle. In *Chaetostoma* usually not quite half the snout is naked, but in *Corymbophanes* the snout is naked all the way to the eyes and to the anterior margins of the nostrils. Another difference is the lack of prickles in *Corymbophanes* on the supraoccipital area forward to and including the interorbital space.

The two species now referred to this genus may be distinguished from each other by means of the following key:

1a. Dorsal rays I, 9 or I, 10; eye  $1\frac{1}{2}$  to  $1\frac{3}{4}$  times in the interorbital space; length of base of dorsal fin much longer than

distance to dorsal origin. (Río Caripe).

*Corymbophanes venezuelae*, new species.

1b. Dorsal rays I, 7; eye in interorbital space 3; length of base of dorsal fin much shorter than eye to dorsal origin. (British Guiana) .....

*Corymbophanes andersoni* Eigenmann

## EXPLANATION OF THE PLATE.

## PLATE I.

Figs. 1, 2, 3. *Corymbophanes venezuelae*, new species. Holotype, U.S.N.M. No. 120,752. Standard length 72.5 mm. Río Caripe, near Caripito, Venezuela.

Fig. 4. *Hypopomus beebei*, new species. Holotype, U.S.N.M. No. 120753. Total length 136 mm. Caripito, Venezuela.



FIG. 1.



FIG. 2.



FIG. 3.

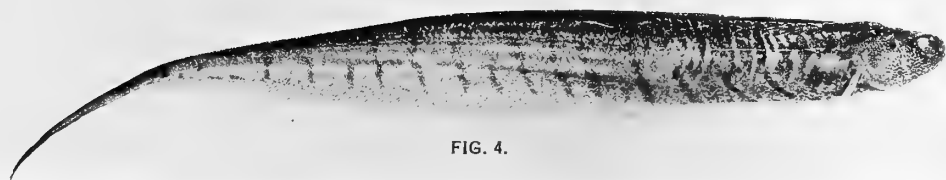


FIG. 4.

TWO NEW SPECIES OF FISHES (GYMNOTIDAE, LORICARIIDAE) FROM CARIPITO, VENEZUELA.





## 6.

A Melanotic Tumor in the Silverside, *Menidia beryllina peninsulæ*  
(Good and Bean).

ROSS F. NIGRELLI &amp; MYRON GORDON

New York Aquarium.

(Plate I; Text-fig. 1).

## INTRODUCTION.

Melanotic tumors in fishes living in a feral state have been reported by several investigators. Osburn (1925) described a tumor of this type from several common bullheads (*Ameiurus nebulosus*) taken from a pond near Falmouth, Massachusetts. This investigator showed that the melanotic tumor was induced by a black pigment-producing coccus. The bacteria was isolated, cultured and the disease reproduced in the skin of apparently normal catfish by injection of the cultivated microorganisms. Other parasites are capable of causing a proliferation of melanophores. Thus, Hsiao (1941) reported a condition of melanosis in a cod (*Gadus collaris*) which was induced by the metacercariae of a heterophyid fluke. Hunter (1941) made further studies on melanophores associated with cysts of similar flukes (*Cryptocotyle lingua*) in the skin of the cunner (*Tautoglabrus adspersus*).

That melanophore proliferation may be correlated with wound healing is indicated by the experiments of Smith (1931, 1932a, 1932b) on goldfish (*Carassius auratus*). He pointed out that mechanical injuries to the skin and exposure to X-rays may cause a response of melanophores which in some cases may be so great as to cause a general but temporary melanosis.

There are other records of melanotic tumors of fishes in the literature, but the etiology of the majority of them is not known. Thus, Ingleby (1929) reported a melanotic neoplasm in an angler (*Lophius piscatorius*). It consisted of chromatophores which were of the same type as those found under the normal epithelium. The pigment cells showed a tendency to spread laterally and to deeper areas of the skin. From this description, it is apparently similar to the melanoma of platyfish-swordtail hybrids, and as will be seen shortly, to that of the silverside as well. Similar cutaneous tumors were

reported by Haddow and Blake (1933) in the thornback ray.

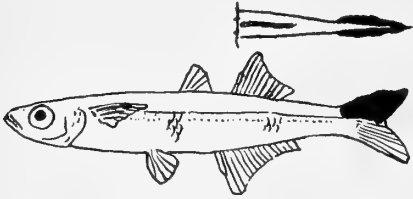
In 1931, Mr. Stewart Springer caught in Biloxi Bay at Iberville, Mississippi, a representative collection of fishes containing many individuals and species. The collection was sent to Dr. Carl L. Hubbs, Curator of Fishes in the Museum of Zoology at the University of Michigan. In sorting and cataloguing the specimens, Dr. Hubbs discovered a silverside with an apparent melanotic tumor. He kindly sent it to us for detailed study. We are indebted to him for the opportunity of making a comparative study of this tumor, which represents a spontaneous growth in a feral fish, with the melanomas of the aquarium-reared platyfish-swordtail hybrids. As Gordon (1941) has pointed out, the melanotic tumors of the platyfish-swordtail hybrids are produced experimentally by genetic methods, specifically by mating a platyfish carrying macromelanophores with a swordtail. Under natural condition in their native habitat, in the rivers of Mexico and Guatemala, *Platy-poecilus maculatus* may occasionally be found living side by side with *Xiphophorus hellerii*—yet in more than 10,000 specimens examined, no hybrids and no tumors were found. Regardless of the mode of origin, it will be shown that the silverside and platyfish-swordtail hybrid melanotic tumors have many characteristics in common.

## DESCRIPTION OF THE TUMOR.

The silverside measured 47 mm. in total length after its preservation in alcohol. The tumor growths covered an area of  $5 \times 1.5 \times 1.0$  mm. (Text-fig. 1) and they extended along the sides of the body in the dorsal region of the caudal peduncle and upper lobe of the tail fin. An examination of all external and internal parts of the body revealed no free or encysted protozoan or metazoan parasites, nor were they discovered after the tumor was sectioned. Except

for the melanotic tumor of the tail region, the fish appeared normal.

In examination of the pigmentary system of the silverside, it was noted that in the region of the lateral line a broad band of melanophores appeared to form a syncytium. Immediately above this line, large melanophores formed a striking reticular pattern merging into an even distribution of melanophores near and at the mid-dorsal line. The melanotic neoplasm was confined chiefly to the lateral line area, extending only slightly below this region. Whether or not the tumor cells were derived from the lateral line melanophores could not be determined.



TEXT-FIG. 1. Lateral and dorsal view of the tide-water silverside showing position and extent of melanoma. Slightly less than natural size. (Drawing by C. Clark.)

The tail region of the fish bearing the tumor was severed from the body and prepared for microscopical examination. After embedding in paraffin, sections were cut at 6 microns. They were stained by a variety of methods, both for bacteriological and general histological detail.

A modified method of Ziehl-Neelson for the detection of acid-fast organisms and the Brown and Brenn technique for the Gram's reaction, as outlined by Gradwohl (1938), were used. Our studies showed that the tissues appeared to be free of bacteria except for an isolated Gram negative bacillus here and there which was not regarded as significant.

Some sections were stained with Ehrlich's hematoxylin, others with Mallory's triple stain. These proved to be of greatest value although Giemsa's stain was employed as well. Histologically, the pigment cell hyperplasia in *Menidia* appeared quite like the melanotic tumors reported for the platyfish-swordtail hybrids by Reed and Gordon (1931) and indicated by them as being in the second state of melanosis. It also resembled the tumor described by Gordon and Smith (1938) in other platyfish species hybrids. The silverside tumor also has many of the features mentioned by Ingleby (1929) for the melanoma in *Lophius*.

The tumor of the silverside contained several sizes of melanin-bearing cells, corre-

sponding somewhat to the size variation found among the melanophores in the corium in normal regions of the fish's body. The pigmented cells in the tumor mass differed from those in the normal corium in that they were not of the precise stellate form of the corial melanophores; rather they appeared amoeboid in shape.

The corium of the tumor masses was almost completely replaced by proliferating pigment-bearing cells and was considerably thickened (Pl. I, Fig. 2; B) as a result of their growth. The boundaries of the melanin-containing cells were not seen clearly owing to the presence of dense deposits of pigment granules. From our study, these apparently active cells seemed to spread laterally in the corial layer and thus might have given rise to other loci with the result that a number of pigmented nodules appeared (Pl. I, Fig. 1; 1, 2, 3). In response to the hypertrophied corial tissues, the epidermis in several places was penetrated by the tumor cells and destroyed (Pl. I, Fig. 2; A). This left the tumor naked at the surface. There was no indication of hemorrhages as described by Reed and Gordon in the platyfish-swordtail melanoma. Surrounding the region of the break-through, the epithelium of the silverside tumor was somewhat thickened and keratinized (Plate I, Fig. 2; C). The epidermal tissue contained many cells full of large clusters of melanin granules, which had some resemblance to engorged macrophages as illustrated and described by Grand, Gordon and Cameron (1941) in their study of fish melanomas in tissue cultures. The presence of large, pigment-filled cells in the epidermis appeared similar to the condition described by Smith (1932a) in the goldfish following injury and healing, and interpreted by him as being part of the process of melanin elimination by macrophages. Another instance of this phenomenon was reported by Gordon and Lansing (1943) in platyfish hybrids.

The silverside melanoma cells arising from the corial nodule penetrated (Pl. I, Fig. 2; D), in several points, the underlying fascia and invaded the subcutaneous areas attacking muscle and bone tissues. In the invasion process the muscle fibers were split and eventually broke down, as indicated by the loss of striation and hyalinization (Pl. I, Fig. 2; E). The invasion route of the tumor cells appeared to follow the path established by the intermuscular tissues. In localized areas, where bone was reached by the tumor cells, the periosteum was also attacked, destroyed and replaced (Pl. I, Fig. 2; F).

In our study of sections stained with Mallory's, sinusoids and capillaries were evident; they were abundant in regions of par-

ticularly large tumor masses. No inflammatory cells were recognizable and a similar condition was reported by Gordon and Smith (1938a) for platyfish-swordtail melanomas. In the melanotic tumor of *Lophius*, however, Ingleby reported the presence of inflammatory cells in the tissues underlying the tumor, but separated from the tumor proper by a broad layer of connective tissue.

SUMMARY AND CONCLUSIONS.

A melanoma in the caudal peduncle and tail region of a feral silverside (*Menidia*) is reported, described and compared with melanotic neoplasms of *Lophius* and platyfish-swordtail hybrids. In several important respects they are quite similar.

The lesions are characterized by an overgrowth of melanin-containing cells which are capable of infiltrating, destroying and replacing epithelium, corium, fascia, muscle and periosteum.

The etiology of the tumor is not known but parasitological and bacteriological techniques employed indicate that a parasitic causative agent is probably not involved in this melanoma.

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**EXPLANATION OF THE PLATE.**

(Photomicrography by S. C. Dunton).

**PLATE I.**

- Fig. 1. Sagittal section through the caudal peduncle and tail of the silverside showing melanotic nodules (1, 2, 3). H.-E. About 25  $\times$ .
- Fig. 2. Higher magnification of a sagittal section through one of the melanotic nodules showing the extent of the lesion. **A**, point where melanin-bearing tumor cells had broken through the epidermis; **B**, thickened corium; **C**, slightly thickened epidermis with massed macrophages containing melanin granules; **D**, the fascia separating corium from muscle is broken and the pigmented cells invade the deeper layers of tissues; **E**, muscle fibers are split and the muscle tissue loses its striation and becomes hyalinized; **F**, bone showing the melanophores massed around the periosteal area; melanophores may also be seen in the region around the dorsal aorta; **G**, Scale. H.-E. 250  $\times$ .



FIG. 1.

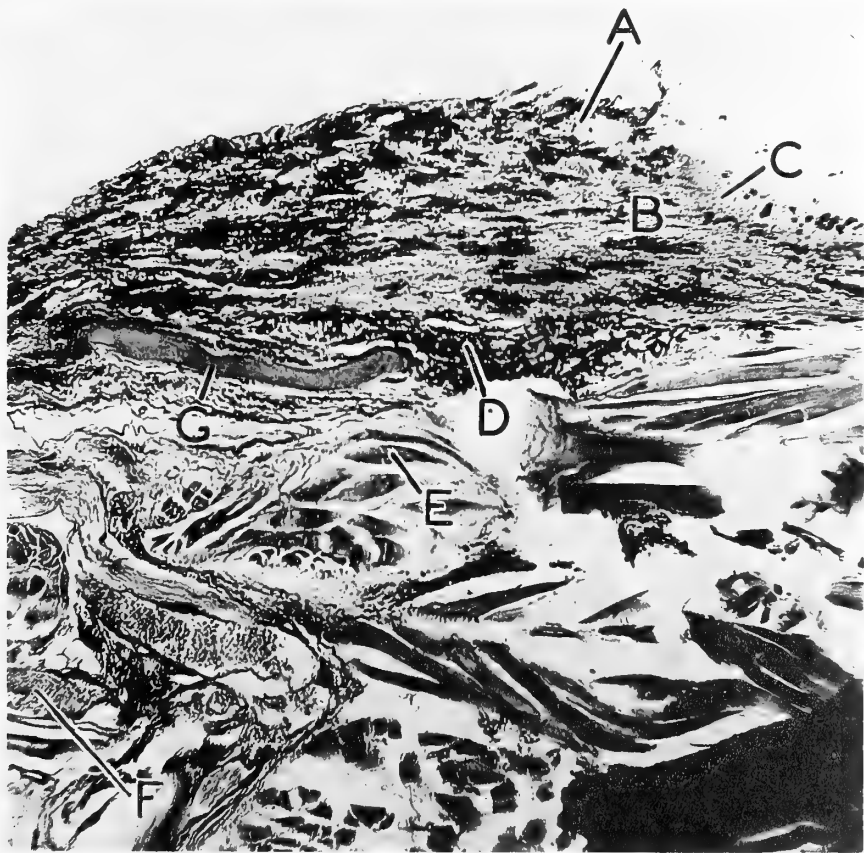


FIG. 2.

A MELANOTIC TUMOR IN THE SILVERSIDE, *MENIDIA BERYLLINA* PENINSULAE (GOOD AND BEAN).



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## 7.

## The Effects of Steroids on the Skeleton of the Poeciliid Fish *Lebistes reticulatus*.

JOSEPH L. SCOTT

Department of Biology, Washington Square College of Arts and Science, New York University.

(Plate I).

The effect of the sex hormones and extracts of the anterior lobe of the pituitary upon the structure of bone has been studied by various investigators. Estrogen-treated mice, guinea pigs, pigeons and chickens have shown, upon histological study of the skeleton, an increased ossification, at least in certain regions. In order to help complete the vertebrate phylogenetic picture, the work reported here was designed to extend this study to fish. The effects of pregnenolone (Pranone, ethinyl testosterone, anhydrodroxy-progesterone) and alpha estradiol (Progynon DH) upon the skeletal structures of *Lebistes reticulatus* (Peters), a fish in which the secondary sex characters are highly responsive to these substances, were determined and are reported here. In this species, the effects of pregnenolone are purely androgenic, but in mammals this steroid substance has various other actions.

The author wishes to express his appreciation to Drs. Robert Gaunt and C. M. Breder, Jr., for suggestions and assistance. He is also indebted to Dr. Max Gilbert of the Schering Corporation for supplying the hormones used in this work. The data presented here are taken in part from a thesis for the degree of Master of Science at New York University.

Ten to fifteen fish were kept in two and a half gallon aquaria. Several plants were grown in each aquarium in an inch of sand. The temperature of the water was controlled thermostatically and ranged from 74°-78° F. Each tank was fitted with a porous stone through which was pumped a steady stream of air. Both treated and control fish were fed, daily, a diet of dried tropical fish food which was supplemented by *Daphnia* and *Tubifex* once a week.

*Lebistes reticulatus*, a viviparous poeciliid with marked sexually dimorphic characteristics, was used as the experimental animal. In this species the anal fin of the adult male is modified to form a gonopodium, the body size of the male is normally smaller than that of the female, and the male only is brilliantly colored. The reaction of these sexu-

ally dimorphic traits of *Lebistes* to the two steroids used here have been previously described by Berkowitz (1) and Eversole (6). Since their results were fully confirmed in the course of our observations no duplicate description is given of them.

A total of 67 fish were treated. Thirty received estradiol, contained in tablets made for human oral use which were powdered and sprinkled on the water. Total dosage varied from 6.5 to 15 milligrams per tank given in equal weekly portions for periods varying from 18 to 110 days. A similar procedure was followed in treating fish with 5-milligram doses of pregnenolone, except that the effects of a single treatment were so long-lasting that monthly administration was more than sufficient to maintain masculinization of all secondary sex characters. In fact, to eliminate effective amounts of the steroid from the tanks a very thorough cleaning had to be done even six months after a dose of the compound was added to the tanks.

Histological studies were made on a segment cut transversely just caudal to the pectoral fin and between the posterior end of the body cavity and the caudal fin. The whole skeleton was studied in total mounts. The material was fixed in Bouin's fluid, washed in 70% alcohol, dehydrated by the dioxan method, and embedded in tissue-mat. Serial sections were cut at 10 microns in thickness and were stained either with Harris' hematoxylin and counterstained with eosin, or with Mallory's triple stain. Whole mounts were prepared by clearing freshly killed fish in KOH until the muscular and skeletal portions were translucent and then staining with Alizarin dye as described by Hollister (10).

Since the treatments given either masculinized or feminized the external sexual characteristics of the animals, the original sex was determined at the end of the experiment by histological examination of the gonads. These were routinely sectioned in the course of other observations. The gonad is itself affected by these treatments (1, 6),

but whether it was originally a testis or ovary was generally easily discernible by its histological appearance, the essential gametogenic elements of which were not changed. The sex ratio of the strain of fish used here is 1:1.

#### OBSERVATIONS.

##### I. Sexual dimorphism in the skeleton.

Cleared whole mounts of normal male and female *Lebistes* showed a skeletal dimorphic character, aside from the difference in size, only in the region of the anal fin or gonopodium (male). The skeleton which supports the anal fin of the adult female (Fig. 2) and of immature fish is composed of a group of ten separate interhaemal bones which project dorsally from the anal fin toward the haemal spines of the first three caudal vertebrae.

Three of the interhaemal bones, the second, third and fourth, are fused as one bone in the adult male (Fig. 1). In addition the first three caudal vertebrae are markedly enlarged and make a sharp angle in the direction of the three fused interhaemal bones.

Most bones in this species are made up of a central cartilaginous mass surrounded by a crust-like ossified layer. No sexual dimorphism in the histology of these structures was noted, except again in the anal fin region where the interhaemal bones of the male contained much thicker ossified layers.

##### II. The effects of hormones upon the skeleton.

All fish, regardless of sex, fed 5 milligrams of pregnenolone at birth, developed typical male structures precociously in the anal fin region described above. There was a fusion of four and sometimes five of the interhaemal bones in the treated animals (Figs. 3, 4, 7). This steroid caused a dwarfed condition in *Lebistes* and consequently the whole skeletal apparatus of the treated fish was reduced in size (Fig. 3). Adult females, given a single feeding of 5 milligrams of pregnenolone, all developed interhaemal bones much like the adult males (Fig. 4) within three weeks. Normal males show this skeletal dimorphism 50-60 days after birth.

Fifteen fish were fed alpha estradiol from birth. All developed a typical female anal fin with the 10 separate interhaemal bones attached (Figs. 2, 6). One group of 9 fish received 3.25 milligrams of the hormone over a period of 50 days. The male controls had begun to show a difference in the anal fin skeleton but not the treated animals. Continuing treatment until 110 days in another series did not vary results.

All of the estrogen-treated fish were studied for the effect upon ossification of the

interhaemal bones. It was found in every case that there was no increase in ossification and these bones had the exact appearance of the female untreated animals (Figs. 5, 6).

On the other hand, all of the fish that were fed pregnenolone, without exception, showed an increase deposition of bone around the central cartilaginous structure of the interhaemal bones toward the condition of the adult male (Fig. 7). The first three haemal spines showed an increase in size which approached that of a normal adult male.

The supporting structures of the gonopodium itself undergo profound changes in the course of sexual maturation in the male. These are induced precociously by pregnenolone, as described by Eversole (6).

The vertebral column was studied carefully for possible effects of hormone treatment. In all of the 67 fish treated with either hormone there was no increase in ossification or other histological changes in the vertebrae, except for the larger spines associated with the anal fin apparatus of the pregnenolone-treated fish.

#### DISCUSSION.

The failure of estrogenic substances in the amounts used here to produce any effect upon ossification is conflicting with the results obtained with this hormone in higher forms. Gardner and his co-workers have reported an increase in endosteal bone formation in birds (12, 14, 15) and mice (7, 8, 24) and some increase in periosteal bone in the pigeon (25). Sutro (21) reported that there was no change in periosteal bone in estrogen-treated mice, although increases in new bone formation of the medullary cavity were noted. The changes in bone formation in rats seemed to be confined to the area round the epiphysis of the long bones, where an increase in the density of this area occurred (Day and Folis, 11). Silberberg and Silberberg (19, 20) found that both estrogens and androgens intensified the ossification of cartilage and increased the deposition of bone in the guinea pig, but that the effects of the androgens were much less intense. Perhaps an explanation for the lack of increased ossification of the estrogen-treated fish is the absence of true endosteal bone and the presence primarily of membrane bone which has been described for certain parts by Mooraker (16). The literature seems to reveal no information at present as to the effects of estrogens upon the membrane bones of higher vertebrates.

Pregnenolone with its androgenic action in *Lebistes*, stimulates ossification in certain of the bones of this fish. This is just the opposite of the effects produced by testosterone in birds and most mammals.

Gardner and Pfeiffer (9) and Turner and co-workers (23) found that testosterone propionate inhibited hypercalcification in the mouse and rat. In ducks, Landauer (15) reported that estrogens caused hyper-ossification even in the presence of testosterone. In view of the difference in size of the two sexes of the guppy, the female being the larger, it would be logical to expect that if sex steroids had any effect on ossification, the androgens would stimulate the process thus stopping growth. However, the well established inhibition of growth in these fish by androgens cannot be attributed to a hyper-ossification, since the latter occurs only in the region of the anal fin.

Finally, it should be pointed out that the regions of the skeleton affected by hormone treatment are exclusively those in which a normal sexual dimorphism exists. The changes induced were in character and extent parallel to that expected from the picture of normal sexual dimorphism. In other words, this fish seems to be refractory to overdosage effects and most parts of its skeleton are probably totally unresponsive to sex steroids, except in generalized size difference.

The variability and specialization in teleost fish is such that experimental results of the type reported here may be applicable only to the species in which they are observed.

#### SUMMARY.

1. Most parts of the skeleton of *Lebistes reticulatus* are not responsive to either estrogenic (alpha estradiol) or androgenic (pregneninolone) sex steroids, except in size. Pregneninolone caused a reduction in skeletal size, associated with a generalized dwarfing, while alpha estradiol produced no clearly significant change in size.

2. Skeletal constituents associated with the anal fin (the gonopod in the male) differ markedly in the two sexes. This anal fin of the immature fish of both sexes is supported by a group of ten separate interhaemal bones. These bones are entirely cartilage in the young fish and in the adult female they are surrounded by a thin layer of membrane bone. In the adult male, these bones are made up of thicker portions of membrane bone than in the female and, in addition, the second, third, and fourth interhaemal bones are fused as one. The male-like condition can be fully developed by androgens in either sex and the female condition can be induced by estrogens.

No changes in the anal fin region could be induced which were greater in extent than those normally seen—that is, there were no apparent overdosage phenomena under the conditions of these experiments.

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## EXPLANATION OF THE PLATE.

### PLATE I.

Figs. 1-4, inclusive, are camera lucida drawings made from whole mounts which had been stained with Alizarin dye. They are all of the same magnification.

Fig. 1. Lateral view of the skeleton of an adult male, in the mid-body region, showing three enlarged haemal spines and the fusion of three of the interhaemal bones. These characters are typical of the mature male.

Fig. 2. Lateral view of the skeleton of an adult female, in the mid-body region, showing small normal haemal spines and ten separate interhaemal bones, typical of the adult female and the immature fish.

Fig. 3. Lateral view of the skeleton, in the mid-body region, of a female guppy fed 5 milligrams of pregnenolone from birth for a period of 21 days showing the enlarged haemal spines of the first three caudal vertebrae and the fusion of 5 interhaemal bones. These characters are typical of the adult male.

Fig. 4. Lateral view of the skeleton, in the mid-body region, of an adult female, treated with 5 milligrams of pregnenolone over a period of 21 days, showing slightly enlarged haemal spines of the first three caudal vertebrae and the fusion of the first 4 interhaemal bones. These are typical male characters.

Fig. 5. A median sagittal section of the mid-body region of an adult female 110 days old, showing separate interhaemal bones with a central cartilage portion which is surrounded by a thin sheath of membrane bone.  $\times 100$ .

Fig. 6. A median sagittal section of the mid-body region of a 110-day-old male treated with 5 milligrams of estradiol from birth. The structure of the separate interhaemal bones is similar to the female control (Fig. 5).  $\times 100$ .

Fig. 7. A median sagittal section of the mid-body region of a female animal treated from birth with 5 milligrams of pregnenolone over a period 21 days showing fused interhaemal bones and a thick layer of membrane bone surrounding the central portion of cartilage.  $\times 100$ .

### ABBREVIATIONS.

H S	Haemal spine.
F I S	Fused interhaemal bone.
A N T	Anterior end of skeleton.
R	Radial bulbous portion of the anal fin to which are attached the fin rays.
I S	Interhaemal bone or spine.
C	Cartilage.
B	Membrane bone.

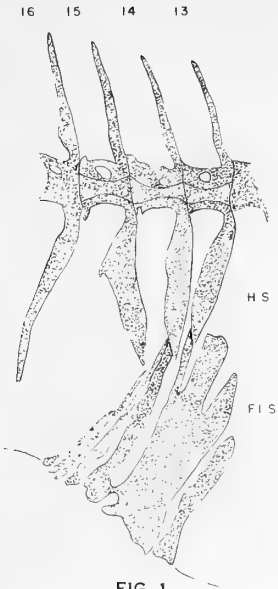


FIG. 1.

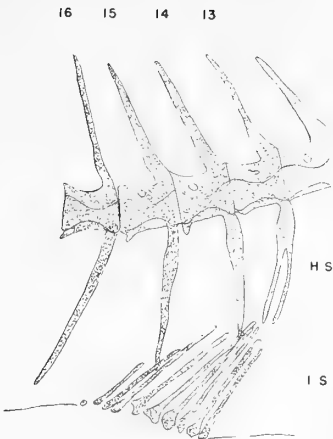


FIG. 2.

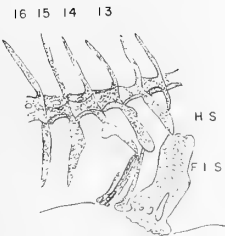


FIG. 3.

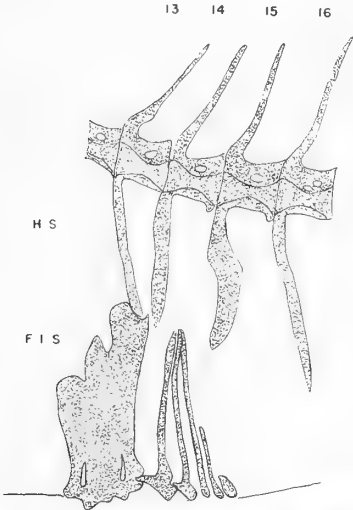


FIG. 4.

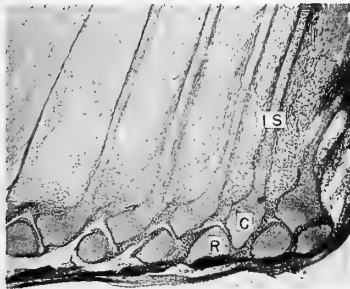


FIG. 5.

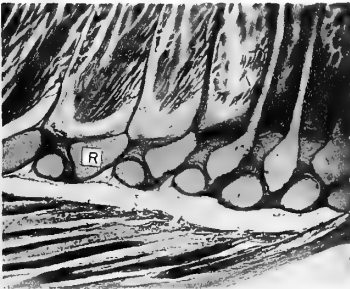


FIG. 6.



FIG. 7.

THE EFFECTS OF STEROIDS ON THE SKELETON OF LEBISTES RETICULATUS.





## 8.

The Function of Secondary Sexual Characters  
in Two Species of Dynastidae (Coleoptera).<sup>1</sup>

WILLIAM BEEBE.

Director, Department of Tropical Research,  
New York Zoological Society.

(PLATES I-V).

[This is a contribution from the Forty-third or Venezuelan Expedition of the Department of Tropical Research of the New York Zoological Society made under the direction of Dr. William Beebe. The expedition was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela. For maps and ecological data see *Zoologica*, Vol. XXVIII, No. 9, pp. 53-59, 1943.]

These notes have to do with two species of dynastids, *Megasoma elephas* Fabr., 1775, and *Strategus aloeus* Linnaeus, 1758. The Venezuelan name for these beetles is *Tornador*, the borer. Another name is *Congarocho*, and in the Andes they are known as *Bobute*.

These so-called elephant beetles were observed and collected at Caripito, north-eastern Venezuela, in the course of the Forty-third Expedition of the Department of Tropical Research of the New York Zoological Society, during a period of seven months, from February to September, 1942. The photographs, both stills and motion-pictures, were taken by Miss Jocelyn Crane, Research Zoologist on the staff of the department.

Only once did I find the big *Megasoma* and the smaller *Strategus* under normal conditions. On March 18 a female of the latter was observed crawling up the trunk of a small jungle tree, and a few days later two male *elephas* were discovered resting beneath an overhanging branch, on a half-rotten log, quite hidden from view.

On March 20 I found a female *Strategus* in a spider web of unusual strength and size, the large rufous-bodied owner frantically wrapping up the struggling beetle. On the

same day, a half-mile away, a member of my staff came across an identical occurrence, only here the victim was a male. All others of both species were taken when flying at night against the screened windows of the laboratory, or around the electric lights in the compound, or on the ground on their backs, in early morning, within the radius of the same lights. Their appearance, however, was only during or after a rain. Fewer than fifty of each species were taken during our whole stay. In *Megasoma* the sexes seemed about equal, but *Strategus* females dominated almost six to one. From the beginning of the rains on April 27, both species became more abundant, several often being taken close together in the mornings beneath the lights of the refinery. None were seen after July 12.

The great development of horns of varying sizes and shapes on the head and thorax of male beetles of the family Dynastidae has long attracted attention and excited speculation. These specialized structures in connection with the great size of the beetles are reflected in many technical names: *Dynastes*, *Megasoma*, *Megaceros*, *Goliathus*, *elephas*, *hercules*, *rhinoceros*, *atlas*, etc.

Charles Darwin in 1871, in the first edition of "The Descent of Man," (Vol. I, pp. 371-372) wrote as follows:

"The extraordinary size of the horns, and their widely different structure in closely-allied forms, indicate that they have been formed for some important purpose; but their excessive variability in the males of the same species leads to the inference that this purpose cannot be of a definite nature. The horns do not show marks of friction, as if used for ordinary work. Some authors suppose that as the males wander much more than the females, they require horns as a defence against their enemies; but in many cases the horns do not seem well adapted for defence, as they are not sharp. The most obvious conjecture is that they are used by the males for fighting together;

<sup>1</sup> Contribution No. 689. Department of Tropical Research, New York Zoological Society.

but they have never been observed to fight; nor could Mr. Bates, after a careful examination of numerous species, find any sufficient evidence in their mutilated or broken condition of their having been thus used . . . The conclusion, which best agrees with the fact of the horns having been so immensely yet not fixedly developed,—as shown by their extreme variability in the same species and by their extreme diversity in closely-allied species—is that they have been acquired as ornaments. This view will at first appear extremely improbable; but we shall hereafter find with many animals, standing much higher in the scale, namely fishes, amphibians, reptiles and birds, that various kinds of crests, knobs and horns have been developed apparently for this sole purpose.”

Eight years later, Alfred Russel Wallace in “Tropical Nature” (p. 372) writes of the “immense horns of some beetles of the families Copridae and Dynastidae, which Mr. Darwin admits are not used for fighting, and therefore concludes are ornaments, developed through selection of the large-horned males by the females. But it has been overlooked that these horns may be protective. The males probably fly about most, as is usually the case with male insects; and as they generally fly at dusk they are subject to the attacks of large-mouthed goatsuckers and podargi, as well as insect-eating owls. Now the long, pointed or forked horns, often divergent, or movable with the head, would render it very difficult for these birds to swallow such insects, and would therefore be an efficient protection, just as are the hooked spines of some stingless ants and the excessively hard integuments of many beetles, against the smaller insectivorous birds.”

Passing by some other comfortably easy explanations we come to the antithesis, given for what it is worth at third hand in “A Year of Costa Rican Natural History” by A. S. and P. P. Calvert (1917). The authors write (p. 69), “Dr. Ohaus has also kindly informed us that a correspondent of his friend Herr Nagel has observed, in Venezuela, that the males of *Dynastes hercules* fight very violent battles among each other for the females; that they seize and crush with the cephalic and prothoracic horns, the weaker male often having its thorax and elytra crushed, and that the victorious males take the females between the horns and carry them away.” This anonymous information coming to us through three subsequent channels requires, I think, considerable confirmation, especially as to the direct crushing power of the horns and the ultimate use of these structures in the Sabine-like kidnapping of the female.

In these and numerous other contributions we have a number of suggestions as to the use of these horns: ornaments, direct

defence against attacks from enemies, and indirect in making ingestion by large-mouthed assailants difficult or impossible, transportation of the female, overdevelopment as sheer, useless impetus of secondary sexual characters, scraping and puncturing bark to induce the flow of edible sap, and fighting among themselves for the possession of the female.

Although I have often kept these giant beetles in vivaria in the tropics, I have never seen, either in free or captive specimens, any confirmation of any of these suggested uses of the horns until April 13, 1942, in the Zoological Society's laboratory at Caripito, northeastern Venezuela.

For a fortnight I had kept three males and a female *Megasoma elephas* in a glass battery jar. The quartet of big beetles had fed steadily on over-ripe banana, their method of feeding being to push and nuzzle into the soft pulp until they were quite plastered with the fruit. In a general cleaning of laboratory cages on this 13th of April I carried the jar and its contents to an outside faucet and held one beetle after another beneath the swift stream of water. When picked up, as usual they turned and twisted, the tearing power of their sharp claws and the pinching strength of head armor against the edge of the thorax making it difficult and painful to hold them. During the process of washing they became quiet and did not move a leg again until returned to their cleansed cage.

I returned the jar to its place, gave the beetles a supply of fresh banana and forgot them until a half-hour later when I heard a confused sound. I found the food neglected and the three males in an intricate pile, massed around the female. I removed her and from this moment on the battling of the males among themselves occupied considerable of our attention. Food was completely ignored in the newly aroused heat of battle. When from exhaustion or other cause the combative instinct died down, I could always initiate new and violent encounters by either an application of the water treatment, or the introduction of a female. Two or three days of enforced drought would reduce the war to casual skirmishes, ineffectual feints, and a renewed interest in the mushy fruit. It seemed more than a coincidence that on April 27, only fourteen days after the transformation wrought by the artificial deluge of the water faucet, the actual rainy season began. In my precocious breaking of the dry season I had anticipated the effect of the annual rains in unlocking the reproductive reactions of these great insects.

Concomitant with this suddenly aroused combativeness was nocturnal activity. From now on we were constantly disturbed by loud drummings and reverberations from the beetles, and found that from dark to

midnight both males and females sought to escape from their cages by flight. The loud banging was due to the impact of the spread elytra against glass and wire, driven by the powerful vibration of the flight wings. This activity ended about twelve or one o'clock and for the rest of the night the beetles rested quietly or fed.

**MATING OF *Megasoma elephas*:** After being drenched with water a pair of beetles would mate almost immediately, whether after long confinement together during which their chief interest was in the banana fodder, or whether both insects had been just caught and placed together. There was no hint of preliminary courtship, no opportunity for appraisal of the horns as ornaments by the female or sexual selection. If no rival was present, the male went straight for the relatively small female and when within reach hauled her toward him, and mating took place at once.

When the male first mounts he wraps his fore legs around the female, sliding them into the lateral crevice between the armor of her head and thorax. In this grip he makes no use of tarsi and terminal claws, but only of the stout, spiny tibia. The second pair of legs hook underneath her body on to the bases of her legs, the terminal claws functioning in this case. When copulation is attained his position changes radically. He now rears almost straight upright, his whole body becoming vertical, resting on his rear tarsi, with the front pair of legs and often the second dangling in the air above the back of the female.

This identical procedure was followed in the first three matings and in a fifth. In the fourth, between a newly caught female and the same male in mating number two, the finale was slightly varied. While the male was in quite as vertical a position, he had shifted the hold of his fore legs, which now clung by the terminal claws of the tarsi to the basal joints of the forelegs of the female, while both second and third pairs of legs dangled free in mid-air. This resulted in a triangular support; his juncture with the female plus the backward pull with his forelegs.

After the water treatment, even if a male was half-immersed in a banana, if a female was dropped into the cage, he instantly became aware of her and rushed in her direction. If a male was substituted the feeding male made no mistake, but, slimy banana and all, went for the new-comer and engaged him head on. In nervousness and quickness his reactions speeded up one hundred per cent. His ordinary activity is a heavy crawling, a slow, bungling creeping with the body dragging. When preparing to mate or fight the body is raised clear and the movements are quick and dynamically directed. In the preliminaries of both

activities there is often a series of rhythmic jerks.

**EGGS:** On May 23 we noticed in the cage which contained five *Megasoma* females that the detritus was in the form of small, rounded balls of dark-colored material, although there was nothing in the enclosure but sections of over-ripe banana. In two cages containing males the excreta was nothing but formless masses of food. I dissolved several of the balls but found no trace of eggs. On May 25, however, Miss Crane discovered the first egg lying loose on the bottom, and after this several appeared every day, but with no relation to the rounded masses of material. Decayed logs put in with the females aroused no interest whatsoever. The eggs measured 4 by 4.7 mm., the surface being smooth, and ivory white.

**FIGHTING OF *Megasoma elephas*:** Although the battle between each individual pair of male beetles is, to a certain extent, slightly different from every other, yet there are several fundamental phases which seem invariable. The opponents meet head on, and either warily wait for the other to attack, or one may rush headlong and begin the encounter. Usually both wait and spar at a little distance. The object first noticeable is an attempt with one or both fore tarsi and claws to trip and unbalance the opponent. This is evident in a long series of single photographs and in several complete kodachrome motion picture sequences. There are quick forward lunges and reachings out with one or both legs, sometimes at the same moment by both insects. This may or may not succeed, but one will force the fighting and the result may be straight pushing and butting for a considerable period, exactly like two antlered deer. Now and then an effort will be noticed to lower the head and get the cephalic horn beneath the other insect. Again and again this is tried, and both may attempt it at the same moment. Then recur the rearing and tripping attempts.

Periods of rest or waiting may intersperse the encounter and twice I have seen one beetle turn and rush after the female. In both cases the other was after him full speed and the battle began again. The female never remained, but went off as far as the confines of the cage, or in the case of the fight taking place in the open, as far as we would allow her to go, when we would recapture her for fear of losing her in the underbrush. The only certainty was that she showed not the remotest interest in the encounter or in either of her suitors. In all our experience with these beetles, which was invariably in the daytime, we never saw either sex take to wing.

Unexpected phases often interrupt the regular succession of the happenings I have

mentioned. The pull of the sharp, curved claws often unbalances both beetles at once and they lose their footing and roll over and over, all twelve legs tangled together and entailing considerable awkward effort before they separate and face each other again. It is astonishing how loud the clash of horn against horn becomes when one's ear is close to the fighters. The insects are usually horizontal when they begin pushing against each other, but attempts at tripping will cause both to rear up high on the second and third pairs of legs. Then, if at all, comes the final phase, the all out attempt to get the tip of the curved bifurcated horn caught in the soft skin of the ventral joint between the thorax and abdomen. Once secured, we realize this is evidently the chief object of the encounter. The successful one puts forth all the strength of which he is capable and lifts again and again with all his might. The higher the other is lifted the more helpless he becomes as his feet, one after the other, leave the ground, and with several super-beetle flings the victim of this grip is thrown over on to his back. Not once, but again and again this was the end result. Often the beetle simply rolled over and came back on his feet again and the whole engagement recommenced, but sometimes he landed on his back and if the surface was at all level and smooth, he spun helplessly waving all six feet in mid-air. The winner began searching in all directions, evidently for the female. Yet if replaced by himself in a cage he soon settled down to immobility.

The whole encounter was reminiscent of the broomstick or cane encounters of our childhood's parties, where the hands of two boys were tied and a cane inserted behind knees and above elbows and the ensuing encounter was, by manipulation of the ends of the stick or otherwise, to roll the opponent over on his back, when he became as helpless as an upset beetle.

The Middleweight Elephant Beetles (*Strategus aloeus*) fought as readily as their larger relations and in almost exactly the same manner. An important difference between the two species is that *Strategus* has all three horns on the thorax, while *Megasoma* has the central curved horn on the head itself. Although thus denied the inter-mobility of the horns, the smaller beetles fought with equal fury and quite as satisfactory results. The general plan of battle was identical, to get the anterior horn beneath their opponent and lever him up and over. In one of the first fights watched there were several momentary lockings and once the attacker was himself pried into the air and almost on his back. When upside down this species seemed even more helpless

than the larger, and I believe would die of starvation on a smooth surface if left to themselves. The general movement and activity was less evident owing to the lack of separate play of horn number one, but there was no lack of fierce effort.

These accounts have been general ones. The following are notes which I took on two individual encounters:

On April 13 two *Megasoma* males after showing desire for battle were placed by themselves in a large open space and they instantly began fighting. They were the two largest of the three which had been kept together for two previous weeks and during that time had, as I have said, shown no great interest in each other or the female, concentrating solely on resting and feeding. This fight was short. The two rushed together and the horns met with a distinct click. For three minutes they pushed, bracing their feet with all possible power. Then separating they did it all over again. The larger one of the two seemed to have the advantage and after three attempts inserted his horn beneath the body of his adversary and actually tossed him clear of himself and the ground. In this case he was on top of the beetle before he could right himself or attempt to do so, and in the ensuing maze of waving legs, the successful male was almost overcome. Again he upset the smaller and again he foolishly helped him to his feet by rushing upon him. At the third and last upset I distinctly saw the horn of the larger beetle push and tear the membrane of the ventral joint, and examination confirmed this damage, slight though it was. A stalemate of pushing ensuing, I separated them for the night.

Disparity in size both between individual males and also sexually is very marked in *Megasoma*. An average male weighs 32 grams and a female 24 grams. The males vary between weights of 28 grams and 36 grams, with corresponding total lengths of 85 mm. and 103 mm. When a number of males are compared they seem to fall into two general nodes to which we gave the names of Major and Minor.

For several days a female and a minor male had been confined together and they had mated. I introduced a major male on May 21, and after righting himself he clambered awkwardly over the small male and toward the female. His antennae played over her back for a few seconds and then the lesser male blundered past him. Like a flash the major turned on the other beetle and the fiercest fight we had seen thus far was on. Both of course tried to get the curved horn under the other, both tried to trip the other off balance. Three times Minor was actually tossed into the air and landed on his back. He levered himself upright and

after the third event he seemed to become thoroughly aroused and fought twice as hard as before. His very smallness of size was a help in some ways and the locked horn gave the larger insect little advantage. Once the giant was turned over and fell on the female and instantly the minor rushed at both and while they were tangled, butted and drove against them and rolled them about. The larger finally got his opponent in a corner and hooked and twisted violently, securing some strange, secure lock and after a wrench we saw the right middle leg of the smaller beetle break off near its base and lie kicking by itself on the ground. Not for a moment did the injured beetle stop his efforts, but I now retrieved him. The same five-legged minor on the following day mated without trouble with two freshly caught females.

After removing the wounded beetle I substituted another major and the combat went on. Both beetles met head on and for at least three minutes, pushing and twisting and jerking with all their might, neither could apparently break the lock. It was like two deer whose antlers have sprung together beyond all possibility of breaking apart. I separated the beetles and found that the apparent locking was due only to uninterrupted pushing, and that in reality the two beetles were quite free to move apart whenever one of them should relax his efforts.

As I said earlier, I neither anticipated nor saw any attempt at carrying the female, and in fact we were unable to push the

large-bodied female between the three horns even temporarily, so that such an improbable feat, as reported in *Dynastes hercules*, seems impossible in the present species.

Even at the height of violent combative activity, I saw no possibility, either in their encounters or in my handling, of any sufficient direct force strong enough to crush or fracture the extremely hard body or elytral armor. The only injuries observed were the slight tearing of the intra thoracic and abdominal ventral membrane, and the snapping of a leg by oblique leverage.

The succession of still photographs of live, unposed beetles taken in two-hundredths of a second presents fairly satisfactory visual realization of this phase of activity of these giant beetles. Proper appreciation of the quickness of movement, the un-scarab swiftness and deftness of use of legs and horns can only be had from the kodachrome motion pictures of the entire conflicts.

**SUMMARY:** Male beetles of two species of Dynastidae, *Megasoma elephas* and *Strategus aloeus*, use their cephalic and thoracic horns for fighting with each other.

The initial stimulus is the beginning of the rainy season. Nocturnal and mating activity are consequent upon individual rains. In captivity both can be aroused to highest pitch and culmination by artificial applications of water.

The phases or methods in fighting in both species are identical, first an attempt to unbalance the opponent by tripping, and then by ventral attack with the anterior horn to lift and throw him upon his back.

## EXPLANATION OF THE PLATES.

These fourteen photographs supplement the verbal portion of this paper, and take the place of the kodachrome motion picture sequences which are limited to a screen. The individual beetles are the same throughout, but three photographs have been interpolated from second and third encounters between the same contestants. These fourteen are selected from a total of sixty-nine. All were taken by Miss Jocelyn Crane.

The battle took place in the compound of the laboratory at Caripito, Venezuela. *Photographic data:* camera, Leica; lens, Leitz 90-mm. Elmar; film, Eastman Super-XX. Figs. 1-7 were made by sunlight alone, exposure 1/60 sec., f:12.5; figs. 8-14 by synchroflash, exposure 1/200 sec., f:16.

A male elephant beetle, *Megasoma elephas* approaches a female (Figs. 1 and 2). While

he prepares to mate, a second male approaches (Figs. 3 and 4). The new arrival attacks (Fig. 5) and separates the mating pair (Fig. 6). The beetles meet head on (Fig. 7) and in their efforts to trip each other, rise on their second and third pairs of legs (Fig. 8). As frequently happens, the tripping is mutually successful and both are upset (Fig. 9). They separate at once. In the course of the continued battle the first male succeeds in getting his cephalic horn beneath the head of his opponent (Fig. 10), and exerting all his strength lifts again and again, raising the beetle clear off his feet (Figs. 11 and 12), and rolling or throwing him over (Fig. 13). With the interfering beetle helpless on his back, beetle number one begins his search for the female (Fig. 14).



FIG. 1.



FIG. 2.



FIG. 3.



FIG. 4.

THE FUNCTION OF SECONDARY SEXUAL CHARACTERS IN TWO SPECIES OF DYNASTIDAE (COLEOPTERA).





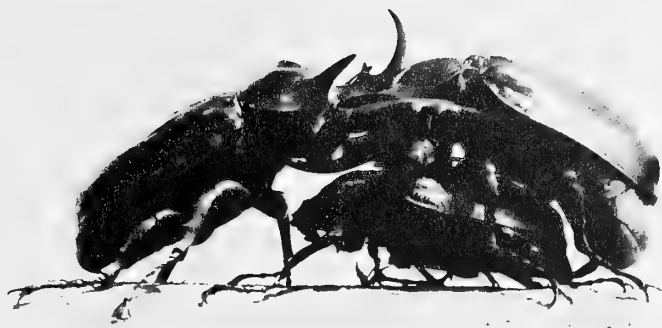


FIG. 5.



FIG. 6.



FIG. 7.

THE FUNCTION OF SECONDARY SEXUAL CHARACTERS IN TWO SPECIES OF DYNASTIDAE (COLEOPTERA).





FIG. 8.



FIG. 9.

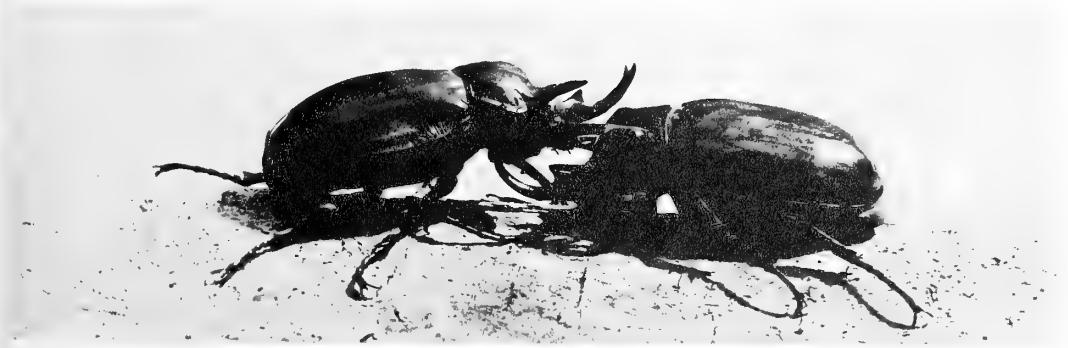


FIG. 10.





FIG. 11.



FIG. 12.

THE FUNCTION OF SECONDARY SEXUAL CHARACTERS IN TWO SPECIES OF DYNASTIDAE (COLEOPTERA).



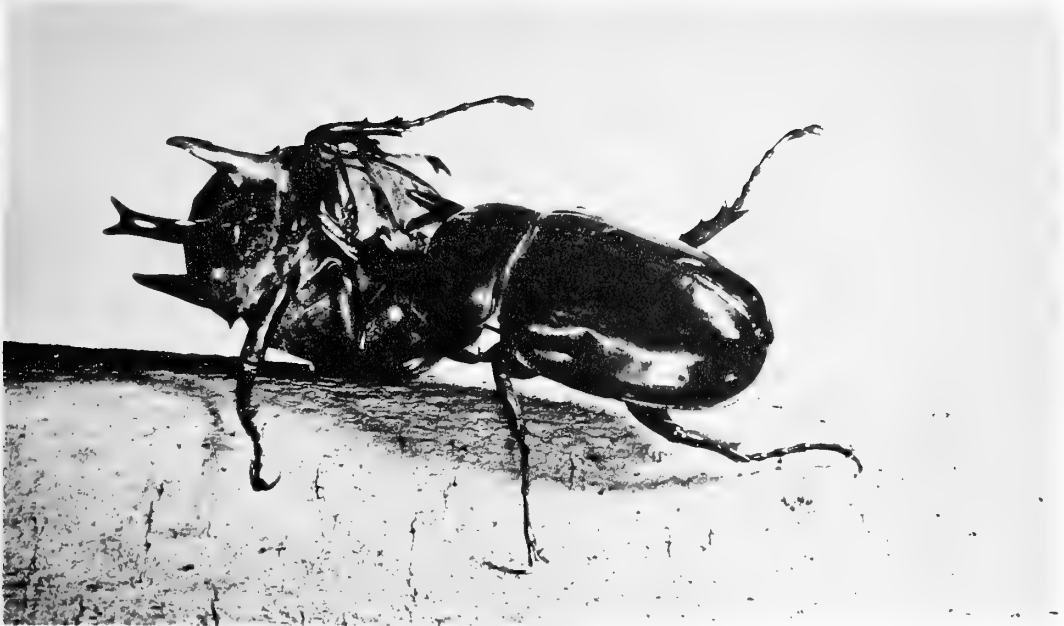


FIG. 13.



FIG. 14.

THE FUNCTION OF SECONDARY SEXUAL CHARACTERS IN TWO SPECIES OF DYNASTIDAE (COLEOPTERA).





## 9.

# Eastern Pacific Expeditions of the New York Zoological Society. XXXIII. Pacific Myctophidae. (Fishes).<sup>1</sup>

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Department of Tropical Research of the New York Zoological Society.

(Text-figures 1-25).

(This is the Thirty-third of a series of papers dealing with collections of the Eastern Pacific Expeditions of the Department of Tropical Research of the New York Zoological Society, made under the direction of William Beebe. The present paper is concerned with specimens taken on the *Arcturus* Oceanographic (1925), the Templeton Crocker (1936), and the Eastern Pacific *Zaca* (1937-1938) Expeditions. For data on localities, dates, dredges, etc., of these expeditions, refer to *Zoologica*, Vol. VIII, No. 1, pp. 1 to 45 (*Arcturus*); Vol. XXII, No. 14, pp. 33 to 46 (Templeton Crocker), and Vol. XXIII, No. 14, pp. 287 to 298 (Eastern Pacific *Zaca*).

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## INTRODUCTION.

This paper is concerned with the Eastern Pacific *Myctophidae* taken off Mexico, Central America and the Galápagos on the Seventeenth, Thirty-fifth and Thirty-eighth expeditions of the Department of Tropical Research sent out by the New York Zoological Society.

The Seventeenth or *Arcturus* expedition in 1925 was in the Pacific for 83 days, during which time 314 deep-sea hauls were

made. The area covered extended from the Gulf of Panama to Cocos Island and the Galápagos, this general area being traversed four times on two round trips. The Thirty-fifth or *Templeton Crocker* expedition in 1936 was of 59 days' duration, and 55 hauls were made along the west coast of California, out to Clarion Island, and from Mazatlan half way up the Gulf of California. The last, *Zaca*, or Thirty-eighth trip in 1937-1938, lasted 145 days. Twenty-seven deep-sea hauls were made from Lower California south along the coast of Mexico and Central America to Gorgona Island. In the course of these three expeditions 10,575 fish of the family Myctophidae were captured, and these resolved into 24 species.

In 1939 Dr. Rolf L. Bolin wrote "A Review of the Myctophid Fishes of the Pacific Coast of the United States and of Lower California." I quote from him, "The area treated in this report is a semicircular segment of the North Pacific Ocean approximately 1,000 miles in radius, having its center a little east of Point Conception, California, and extending from Cape Flattery, Washington, to Cape San Lucas, Lower California, including the Gulf of California."

Within this area Bolin records 20 species of myctophids, derived from various collections and museums (Bolin, 1939). One of these, *Scopelogadus tristis*, I hesitate on known evidence to admit within the family Myctophidae. Of the remaining 19, 12 species occur in our collections. All of the remaining seven which we did not capture, appear to be essentially northern forms, none having been taken south of 31° 33' N. Lat., or the boundary between California proper and Lower California. This is also the northern limit of our collecting.

The seven northern species in Bolin's list and not in ours are, *Electrona crockeri*, *Tarletonbeania crenularis*, *Diogenichthys scofieldi*, *Lampanyctus leucopsarus*, *Lampanyctus nannochir*, *Lampanyctus steinbecki* and *Lampanyctus regalis*.

The deep-sea family of lanternfishes or Myctophidae appears to be second in abun-

<sup>1</sup> Contribution No. 690, Department of Tropical Research, New York Zoological Society.

dance among all other abysmal fish. In my "Preliminary List of Bermuda Deep-sea Fish" (Beebe, 1937) I recorded the fact that the 57 species of Myctophidae composed about 25 per cent. of the entire list of deep-sea species, while the total count of specimens, amounting to about 12,000, was 10 per cent. of the entire catch.

This family was exceeded only by that of the genus *Cyclothone* of the family Gonostomidae, which, with only three species or 1 per cent. of the whole, in individuals amounted to nearly 94,000 or 82 per cent.

In the Pacific, proportions of actual numbers are of no comparative value, owing to the fewer number of hauls (396 compared with 1,500), much shorter time involved, and a widely scattered area compared with a concentration within an eight-mile circle.

On the three Pacific expeditions I took 10,575 myctophids of 24 species, whereas cyclothones were obtained in relatively much fewer numbers than in the Atlantic. The relation between myctophids, cyclothones and other bathypelagic fish in the two oceans as represented in the catches on my expeditions are clearly shown in the accompanying diagrams. (Text-fig. 1).

	ATLANTIC	PACIFIC
Myctophids	10,008	10,575*
Cyclothones	95,189	15,500
Other fish	10,550	2,200
Totals:	115,747	28,275

As to specific abundance in the two oceans, in the Pacific *Myctophum coccoi* (4,466) is far ahead, with *M. affine* next (3,708), and *M. laternatum* third (1,171). In the Atlantic, *M. laternatum* is first (2,853), and *M. benoiti* second (1,294). *M. coccoi* and *M. affine* are well down the list.

\* Out of this total, 4,460 were *coccoi*, all taken on the *Arcturus*, as compared with 165 taken in Bermuda.

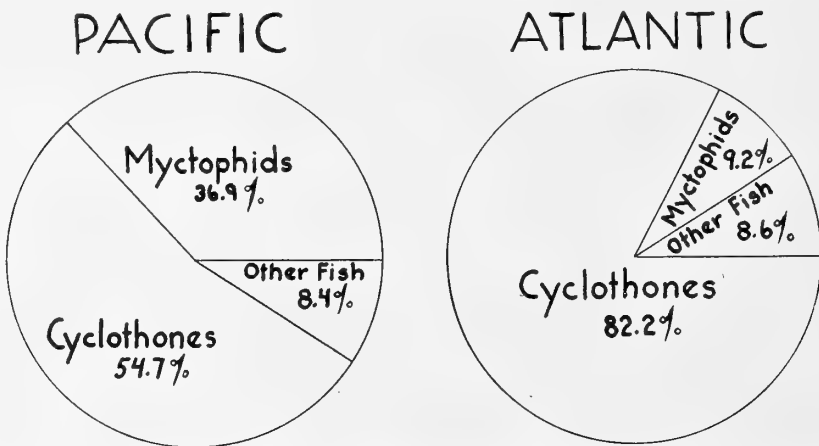
On the Templeton Crocker expedition the southern limits were Clarion Island, Cape San Lucas and Mazatlan. In 55 hauls we took 346 myctophids of eight species, all of which were collected on one or both of the other trips. Two species (*M. laternatum* and *L. mexicanus*) out of the seven, comprised 89 per cent. of the whole.

On the *Zaca* trip which included the whole of Lower California and south to Gorgona Island, in the course of 27 hauls, 621 myctophids were captured, of 15 species. Here again, two species (*M. laternatum* and *L. omostigma*) predominated, and formed 86 per cent. of the entire catch. Four species (*M. pterotum*, *L. idostigma*, *Diaphus dumerili* and *D. pacificus*) were not taken on the other trips.

On the *Arcturus* trip which was concentrated in the comparatively limited area between Panama and the Galápagos, 314 hauls yielded 9,608 individual myctophids, resolving into 19 species. For the third time, two species (*M. affine* and *M. coccoi*) were so abundant that they totalled 84 per cent. Nine species (*M. rarum*, *M. valdiviae*, *L. elongatus*, *L. longipes*, *L. macdonaldi*, *L. macropterus*, *L. tenuiforme*, *L. townsendi*, and *D. gemellari*) were confined to the hauls of this expedition.

In regard to the general distribution of the 24 species taken by us, 14 are cosmopolitan (*M. affine*, *M. coccoi*, *M. laternatum*, *M. pterotum*, *M. reinhardti*, *M. valdiviae*, *L. elongatus*, *L. longipes*, *L. macropterus*, *L. tenuiforme*, *L. townsendi*, *D. dumerili*, *D. gemellari* and *D. rafinesquii*). Three of these have a restricted distribution in the Pacific (*L. longipes*, and *D. gemellari* only in the Galápagos, and *M. valdiviae* only in Japan and the Galápagos).

Eight more species have so far been found only in the Pacific. Five of these are limited to the Eastern Pacific (*M. aurolaternatum*,



TEXT-FIG. 1. Relative percentages of deep-sea myctophids, cyclothones and other bathypelagic fish taken in the Pacific and in the Atlantic.

*L. mexicanus*, *L. idostigma*, *L. ritteri*, and *D. pacificus*). One reaches Hawaii (*L. omostigma*), and two extend as far as the western boundary of this ocean (*M. californiense* and *M. evermanni*).

The remaining two myctophids have the rather curious distribution of Galápagos and the Atlantic (*L. macdonaldi* and *M. rarum*).

These facts must always be held suspect and tentative from the fragmentary knowledge which is implied by the necessarily sporadic character of the results of deep-sea trawling.

A few facts may be gleaned from the record of breeding females and the total number of eggs ready to be deposited. The height of the breeding season seems to be about June 1, with scattered instances from May 11 to 25 and more rarely as early as April 12. I have no notes between July and November.

Graded on number of ripe eggs we have the following list of selected examples:

TOTAL EGGS	DIAM. LENGTH		SPECIES
	ETER MM.	FEMALE MM.	
120	.28	22	<i>Myctophum valdiviae</i>
400	.45	25	<i>Myctophum laternatum</i>
1200	.3	55.5	<i>Myctophum affine</i>
2400	.27	76	<i>Myctophum aurolaternatum</i>
2700	.28	59	<i>Lampanyctus omostigma</i>
3300	.25	50	<i>Myctophum coccoi</i>

Correlation of number of eggs with size of female seems the only outstanding fact, and to a less degree a relation between the total eggs and their relative diameter.

One feature which I hope will be of service to future workers in the field of Pacific myctophids is the brief annotation of data from the various bibliographies, which has been painstakingly excerpted by the junior author.

In the present study, the criterion of adulthood is based on the presence of luminous glands combined with relative size and other superficial external characters. This method necessarily includes many slightly immature individuals which, if classified as in my previous deep-sea papers, would have been considered "transitional adolescents," since in those the term "adult" was reserved for individuals which were found on dissection to have mature gonads. This simplification of the usual growth stage analyses into merely "young" and "adult" was necessitated by present practical difficulties in examining in greater detail such large numbers of specimens. Numerous post-larval and other extremely immature myctophids lacking all photophores were not included in this study.

By "length" is always understood standard length, measured from the tip of the

snout to the end of the vertebral column at the base of the caudal fin.

Abbreviations of trawling apparatus are as follows: T=ordinary meter net; Pt=Pettersen trawl; Ot=otter trawl; L=surface light.

WILLIAM BEEBE

TABLE I.  
NUMERICAL TABULATION OF SPECIES COLLECTED ON THE THREE EXPEDITIONS TREATED IN THIS PAPER.

SPECIES	TEMPLETON			TOTAL
	ARCTURUS	CROCKER	ZACA	
<i>Myctophum affine</i>	3,675	1	32	3,708
<i>aurolaternatum</i>	113	3	9	125
<i>californiense</i>	...	5	8	13
<i>coccoi</i>	4,460	3	3	4,466
<i>evermanni</i>	105	...	3	108
<i>laternatum</i>	617	129	425	1,171
<i>pterotum</i>	...	...	6	6
<i>rarum</i>	1	...	...	1
<i>reinhardti</i>	131	24	1	156
<i>valdiviae</i>	35	...	...	35
<i>Lampanyctus elongatus</i>	3	...	...	3
<i>idostigma</i>	...	...	12	12
<i>longipes</i>	1	...	...	1
<i>macdonaldi</i>	3	...	...	3
<i>macropterus</i>	137	...	...	137
<i>mexicanus</i>	36	177	4	217
<i>omostigma</i>	246	...	94	340
<i>ritteri</i>	19	...	1	20
<i>tenuiforme</i>	5	...	...	5
<i>townsendi</i>	1	...	...	1
<i>Diaphus pacificus</i>	...	...	19	19
<i>dumerili</i>	...	...	3	3
<i>gemellari</i>	1	...	...	1
<i>rafinesquii</i>	19	4	1	24
Totals:	9,608	346	621	10,575

MYCTOPHIDAE COLLECTED BY THE  
EASTERN PACIFIC EXPEDITIONS.

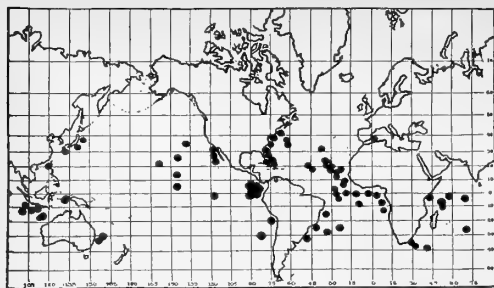
*Myctophum affine* (Lütken, 1892).

*Specimens taken by Eastern Pacific Expeditions:* 3,675 specimens; *Arcturus* Oceanographic Expedition; surface to 800 fathoms; between 2° 00' S. and 6° 58' N. Lat., and 83° 34' and 91° 53' W. Long.; lengths 15 to 67.5 mm.; between March 31 and June 19, 1925.

1 specimen; Templeton Crocker Expedition; at the surface; 25° 02' N. Lat., and 115° 52' W. Long.; length 22 mm.; May 19, 1936.

32 specimens; Eastern Pacific (*Zaca*) Expedition; surface to 500 fathoms; between 4° 30' and 28° 42' N. Lat., and 78° 35' and 117° 50' W. Long.; lengths 6 to 66 mm.; between Nov. 8, 1937, and March 25, 1938.

*Specimens previously recorded:* 296 specimens; ? to 96 mm.; 0 to 1,914 fathoms; north and south Atlantic, Mediterranean, Indian Ocean, Japan, East Indies, Tasman Sea, Hawaiian Islands, central and eastern Pacific from lower California to Chile.



TEXT-FIG. 2. Distribution of *Myctophum affine*.

*Photophore count and variation:* 42 males, 21 females and 421 young fish examined as to relative number of photophores on both sides of the body. The mean is very evidently 8-5 on both sides of the body, as 221 out of the 484, or 45.6 per cent., possess this combination. The extremes in numbers are 6-9 and 4-6. Parr in counts on Atlantic specimens found as many as 10 in the anterior, and as few as 3 in the posterior AO.

In addition to the dominant pattern of 8-5, only seven other numbers are found which show symmetrical lateral distribution, 7-4, 7-5, 7-6, 8-4, 8-6, 9-4 and 9-5. The remainder fall irregularly into a total of 31 variations on the two sides. The three groups show no age or sexual differences in total numbers or in variations of photophores.

*Luminous glands:* The youngest fish in which traces of male, supracaudal luminous glands are visible, measures 29 mm., and shows two glands. The youngest female with glands showing is 34.5 mm. in length, and also has two glands. The largest male, 66 mm., has seven glands, and the largest female of 67.5 mm. possesses four glands. This gradual increase in both sexes with age, is confirmed by five-millimetre successive averages as follows: males, from 29 to 66 mm. 2, 3.2, 3.6, 3.8, 4, 5, 5.5 and 7 glands; females, from 34.5 to 67.5 mm. 2, 2.15, 2.25, 3 and 4 glands.

Three specimens taken on the *Arcturus* expedition (Cat. Nos. 5281, 5281a and 6059; lengths 44, 54.5 and 59 mm.) show both supra- and infracaudal luminous glands. The first shows an unusually small number of photophores, viz: 7-5, 7-5; and the third fish possesses almost the highest number, 9-5, 9-6. No. 5281 shows two dorsal and two ventral glands, No. 5281a has two dorsals and three ventrals, and No. 6059 has two dorsal and five ventral glands.

*Sex proportions:* Out of the total of 3,708 specimens collected, 63 are adult; 42 males and 21 females, a proportion of two to one.

*Breeding:* Two egg counts are as follows: Female No. 5281c, length 51.5 mm.; taken April 12, off Galápagos; total egg count, both ovaries ca. 1,400, eggs measuring .34 mm. in diameter. Female No. 6058b, length

55.5 mm.; taken June 1, off Cocos Island; total eggs ca. 1,200; .3 mm. in diameter.

*Anatomy:* Typical adult male, No. 6058a, taken with above female (No. 6058b) and two young at Station 74, surface haul T-35. Length 54.5 mm.; air bladder large, 14.5 by 4.5 mm.; stomach heavily pigmented with black, 7.5 by 2.2 mm. (for food see separate section). The pyloric opening surrounded, at a distance of 3 mm. along the gut, by 9 caeca, which measure from 3 by .8, to 4.5 by 1.1 mm.

The intestine has but one convolution to break the straight line from the point at which the caeca enter it to the anal opening; total length 20 mm. The testes measure 13 by 1.5 mm. and lie along the ventral side of the air bladder. The kidney occupies the space between the slightly pigmented lining of the body cavity and the vertebral column, and thickens anteriorly to form a large lobe over the stomach. Pouch of gut from which the pyloric caeca open with two large nematode parasites.

The accompanying female (No. 6058b) possesses 11 pyloric caeca. Seven parasitic worms coiled partly in caeca, in pouch and also in upper intestine.

*Development:* Of the total catch of this species, 3,645 are young, showing no signs of luminous glands, and measuring from 6 to 27.5 mm. in length; 42 males measure 29 to 66 mm.; and 21 females measure from 34.5 to 67.5 mm.

*Vertical distribution:* Of the 3,708 specimens, the vertical distribution is as follows:

DEPTH FATHOMS	No. OF FISH
0	3,286
200	406
400	8
500	6
800	2

The surface fish were all taken after dark, with the exception of 21 individuals, comprising one-half of one per cent., all young, which were captured at the surface in daylight.

This would indicate that *Myctophum affine* is essentially a nocturnal surface swimmer (88 per cent. of the entire collection being captured at this level), descending to extremely dark depths (200 fathoms maximum) during the hours of daylight. As the nets were non-closing it seems likely that the 16 fish taken at 400, 500 and 800 fathoms, may actually have entered the nets on their way to the surface.

*Sociability:* Seasonally, at least, it would seem certain that *Myctophum affine* lives in large schools. As will be seen from the accompanying table, nine nets contained from 100 to 1,100 fish each. These totalled 3,213, or 86 per cent. of all this species collected. Especially significant is the fact that eight

of these nine hauls were made between April 14 and 29. All the fish in these captured schools were young, except for 16 adults taken in the single non-April haul of June 13. Also all except one net was a surface haul, and that contained 406 fish from 200 fathoms.

DATE	NO. OF FISH	DEPTH FATHOMS	CAT. No.
April 12	124 Young	0	5281
April 14	280 Young	0	5234
April 15	266 Young	0	5332
April 20	1,100 Young	0	5373
April 21	406 Young	200	5507
April 22	456 Young	0	5387
April 23	111 Young	0	5424
April 29	306 Young	0	5507
June 13	164 (148 Young) ( 14 Males) ( 2 Females)	0	6399

Aside from the above nets, 52 others averaged only eight fish to a haul, and in 17 there was only a single fish each.

*Food:* The stomachs of 10 specimens contained only copepods, with a few small amphipods and fish eggs.

*Luminescence and viability:* Three notes on the lights of this species will show the more usual reactions after capture. A 19 mm. individual was taken at Station 30 T-1, Cat. No. 5133. In an aquarium it survived for ten minutes. For a considerable time it showed no light and then the entire fish was outlined by almost every one of the 80-odd organs. Then it would become completely dark and light up again, this occurring about every 15 seconds. Rarely several spark-like rays shone forth, penetrating, clear and brilliant. I happened to lift my wrist watch with its dully luminous dial close to the fish and it reacted at once, giving out two strong discharges of the caudal glands. Concealing the watch and later displaying the light of its face resulted in instant reaction. This happened eight times. I then flashed on my much stronger flash-light with no result. For five minutes I alternated the two artificial sources of illumination with identical results, the fish reacting vigorously to the watch dial, but paying no attention to the electric torch.

From the haul Station 63 T-1 a 20 mm. myctophid was taken to the dark room, but although apparently dead, throughout ten minutes it showed only one source of light, that from the pair of terminal, sub-mandibular, branchial organs. Twenty other fish were lively. At first the presence of numerous *Noctiluca* and *Sapphirina* made accurate observation difficult, but when clear water was substituted, two general types of illumination were distinguishable, an indirect glowing, constant but impossible to restrict to any organ or group of organs. The entire fish glowed with a generalized light, the

scale mirrors gleaming in a marvelous manner, which gave the appearance of coming from some outside source in the room, were it not that I was sitting in absolute darkness. The other lights were sudden, abrupt, short, sharp, distinct flashes as from a make-and-break apparatus. After an hour of watching, when rigor mortis seemed to have set in, and all movement had ceased, a short renewal of the lights could be brought about by shaking the water or pinching the fish.

Net T-2 of Station 88 on the *Arcturus* was a surface haul made at 9 P. M. on June 13, 1925, three miles north of the island of Albemarle, Galápagos. A number of full grown *Myctophum affine* were taken at once down to the dark room where they darted about a small aquarium. A slight tap on the glass was sufficient to increase the constant luminescence of the lateral photophores, but this light was at all times so steady that it was easy to distinguish every organ and hence to make certain of the species. The lumination was light yellowish-green, as near as I can give it a name. As the fish grew weaker this light did not die out but became dull and indistinct.

The ventral batteries were stimulated irregularly and unexpectedly. It was difficult to say whether a tap on the glass, or collision with another fish, or some unidentifiable emotion was the cause, or perhaps all three at various times. As with other species of this genus, I never saw the secondary sexual caudal lights function when the fish was alone; only when several were together and in a state of excitement or fear, as on the first introduction to an aquarium, or at a sudden disturbance due to the adding of more water or fish. Under normal conditions of environment this light may well have a sexual function, as in attracting the opposite sex, but in the narrow, artificial confines of an aquarium, its principal effect on human spectators was a momentary blinding, with immediate visual disappearance of the fish. The power of this glandular light is very much greater than that given off by all the other organs together. The entire dark room was momentarily illumined when the supra- or infracaudal glands flared out. There seemed no difference in intensity between the light of the males or females.

In daylight the general appearance of the fish was deep purple, in sharp contrast to the brilliant silver scales of *Myctophum coccoi*.

STUDY MATERIAL.

A total of 3,706 specimens was taken, as follows: *Arcturus* Expedition, Station 30 T-1(1); 31 surface(1); 33 T-2(35); 38 T-1(6); 38 Pt-2(1); 39 T-1(1); 39 T-2(8); 39 T-3(124); 39 T-5(3); 41 T-1 (6); 41 T-3(279); 45 T-1(266); 47 T-1(1100); 49 T-1(406); 49 T-2(1); 50 T-2(1); 50

T-5(456); 52 T-1(38); 52 T-1(1); 52 T-1(2); 52 T-2(111); 52 T-3(3); 53 T-3(4); 57 T-1(306); 62 T-1(1); 63 T-1(1); 63 T-1(10); 65 Ot-1 and T-3 and T-4(2); 65 surface(8); 74 T-1(1); 74 T-23(17); 74 T-26(2); 74 T-29(2); 74 T-35 to T-40(4); 74 T-41(8); 74 T-43 and T-44(4); 74 T-61 to T-66(3); 84 T-2(1); 84 T-5 and T-6(5); 84 T-14(1); 84 T-16(1); 84 T-16(13); 84 T-15 to T-17(61); 85 T-1(30); 86 T-4(2); 86 T-7(1); 86 T-8(1); 87 T-2(4); 87 T-3(1); 87 T-6(1); 88 T-1 and T-2 to T-4(164); 88 T-1(3); 88 T-2(2); 88 T-3(20); 88 T-4(5); 90 T-1 and T-2(18); 91 T-1(28); 91 T-1 and T-2(12); 91 T-2(29). Templeton Crocker Expedition, Station 170 L-1(1). Eastern Pacific (*Zaca*) Expedition, Station 177 L-1(2); 225 T-1(1); 227 T-1(3); 228 T-1(1); 231 L-1(25). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 110).

#### *Scopelus affinis*:

Lütken, 1892, p. 252, fig. 10. (Brief description; key; ? to 37 specimens, including type; ? mm.; ? fathoms; mid-Atlantic, off south Africa, Indian Ocean).

#### *M. (Myctophum) affine*:

Brauer, 1903, p. 190, figs. 105-7. (*partim*: Synonymy and description; ? to 76 specimens; ?-78-? mm.; 380 to 1,914 fathoms; Gulf of Guinea, Cape Verde, Bay of Bengal, Indian Ocean, Seychelles Islands).

Zugmayer, 1911, p. 27. (1 specimen; 34 mm.; ? to 275 fathoms; Mediterranean).

Pappenheim, 1914, p. 193. (4 specimens; 15 to 19 mm.; ? fathoms; north Atlantic, near Cape Verde, mid-south Atlantic).

Bolin, 1939, pp. 92, 110, fig. 11. (Key and description; 9 specimens; 28.7 to 72 mm.; ? fathoms; open Pacific, off Guadalupe Island, Atlantic Ocean).

#### *Myctophum opalinum*:

Goode & Bean, 1895, pp. 72, 511, fig. 81. (61+ specimens, including types; ? mm.; 104 to 1,536 fathoms; northwest Atlantic).

Jordan & Evermann, 1896, p. 571. (Brief description).

Waite, 1904, pp. 153, 193. (1 specimen; 95 mm.; ? fathoms; Lord Howe Island, near Australia).

Breder, 1927, p. 17. (? specimens; 25 to 50 mm.; ? fathoms; West Indies).

#### *Myctophum nitidulum*:

Garman, 1899, p. 266, pl. LVI, fig. 3. (Type description; ? specimens; ? mm.; ? fathoms; northwest of Hawaiian Islands).

#### *Rhinoscopelus oceanicus*:

Jordan & Evermann, 1903, p. 68, fig. 15. (General description; 2 specimens; type and co-type; 25 mm.; surface; near Hawaii).

#### *Myctophum margaritatum*:

Gilbert, 1905, p. 596. (General description; ? specimens, including type of 80 mm.; surface; near Hawaii).

#### *Myctophum affine*:

Goode & Bean, 1895, p. 72. (Brief description).

Jordan & Evermann, 1896, p. 570. (Brief description; key).

Lönnberg, 1905a, p. 63. (1 specimen; ? mm.; surface; South Atlantic, off Brazil).

Gilbert, 1908, p. 217. (Brief discussion of range and anal photophores; ? specimens; ? mm.; ? fathoms; mid-Pacific, south to Marquesas).

Gilbert, 1911, p. 14. (Name listed; 1 specimen; ? mm.; ? fathoms; west of Galápagos).

Gilbert, 1913, pp. 75, 76. (Key and discussion of anal photophores; 17 young specimens; ? fathoms; Japan).

Gilbert, 1915, p. 312. (Synonymy and distribution; 1 young specimen; surface; Catalina Island, off coast California).

Weber, 1913, p. 87. (Synonymy and distribution; 2 specimens; 14 mm.; ? to 821 fathoms; Banda Sea).

Weber & Beaufort, 1913, p. 161. (Synonymy and description).

Jordan & Jordan, 1922, p. 11. (Name listed).

Parr, 1928, pp. 65, 69-74, figs. 8, 9. (Key; synonymy; general and detailed description, including study of light and dark pigmentation; 32 specimens; ? mm.; surface; Bahamas).

Parr, 1934, p. 45. (Synonymy).

Taning, 1928, p. 53. (Key to species).

Fowler, 1928, p. 69, fig. 13. (Synonymy and description).

Norman, 1929, p. 514. (Brief reference).

Norman, 1930, p. 325. (8 specimens; 12 to 30 mm.; surface to 300 fathoms; south Atlantic).

Beebe, 1929, p. 15. (Preliminary listing; 4 specimens; ? mm.; surface to 800 fathoms; Hudson Gorge, North Atlantic).

Beebe, 1937, p. 204. (Preliminary listing; 37 specimens; 13 to 25 mm.; 400 to 1,000 fathoms; Bermuda).

LeGendre, 1934, p. 336. (Key to species).

#### *Myctophum aulaternatum* Garman, 1899.

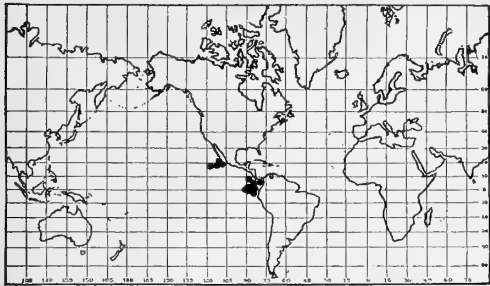
*Specimens taken by Eastern Pacific Expeditions*: 113 specimens; *Arcturus* Oceanographic Expedition; surface to 800 fathoms; between 2° S. and 6° 40' N. Lat., and 80° 48' and 91° 53' W. Long.; lengths 18 to 82.5 mm.; between April 12 and June 19, 1925.



3 specimens; Templeton Crocker Expedition; at the surface; between 18° 44' and 22° 30' N. Lat., and 110° 15' and 114° 20' W. Long.; lengths 31 to 80 mm.; between May 7 and 9, 1936.

9 specimens; Eastern Pacific (*Zaca*) Expedition; surface to 500 fathoms; between 4° 30' and 9° 15' N. Lat. and 78° 33' and 85° 10' W. Long.; lengths 21 to 37 mm.; between Feb. 7 and March 26, 1938.

*Specimens previously recorded:* 31 specimens; ? to 90 mm.; surface; mouth of the Gulf of California and off Panama. Our specimens extend the range south to Cocos Island and the Galápagos.



TEXT-FIG. 3. Distribution of *Myctophum aurolaternatum*.

*Photophore count and variation:* Out of the total of 125 fish taken, 115 were available for photophore counts, the remaining 10, from 18 to 23 mm., being too young to show any trace of these light organs. In the 115 fish there were 21 different combinations of the anterior and posterior AO photophores, 11 of which were asymmetrical, showing different combinations on the two sides. With 10 symmetrical variations, the balance between the two was much more even than in *Myctophum affine*.

There were two very evident numerical nodes, 10-6, 10-6; and 11-6, 11-6, with 16 fish showing the first, and 29 the latter arrangement. Fifty per cent. of the fish presented one or the other of these two combinations. The extremes in actual number of photophores were 9-6, 9-6 totalling 30, and 12-6, 12-6 with a total of 36. Far from showing any correlation with age, the smallest (18 and 20 mm.) and the largest (82.5 mm.) shared the largest number of photophores.

*Luminous glands:* Out of a total of 125 fish, only 11 showed evidences of the supra- and infracaudal luminous glands, of which six were males and five females. Unlike the condition in *Myctophum affine* there was no correlation of size with number of glands, the males showing 45 mm. (5 glands), 60 mm. (7), 66 mm. (6), 70 mm. (9), 75 mm. (8), and 80 mm. (7 glands). In a 68 mm. female the glands were barely discernable, while a 70 mm. male and female each had

9 well developed. Bolin records a fish of 60.5 mm. showing no trace of the glands.

*Sex proportions:* As already stated, of the 11 specimens with sexually distinct luminous glands, six were males and five were females.

*Breeding:* Three dissected fish showed the following conditions: Female No. 5539, 68 mm. in length, taken April 23 off the Galápagos, had the infracaudal glands barely discernable, and the ovaries with no enlarged eggs, showing no signs of imminent breeding.

Female No. 25580, 80 mm. long, captured on May 8, 180 miles southwest of the tip of Lower California, had four small caudal plates, and the ovaries quiescent, with no enlarged eggs.

Female No. 6059, 76 mm. long, taken June 1, 60 miles south of Cocos Island, showed three well developed infracaudal glands. The ovaries were in breeding condition, with approximately 1,200 eggs in each ovary, large and about to be laid. Scattered among them were many very small eggs.

*Development:* Out of 125 fish taken, 114 were glandless young, measuring from 18 to 41 mm. Eleven showed the glands of sexual differentiation, 45 to 82.5 mm. lengths, although these are not necessarily to be classed as full-grown adults (see under *Breeding*).

*Vertical distribution:* All 125 specimens of *Myctophum aurolaternatum* were taken at the surface after dark, or at depths which negated surface conditions of sunlight. In all, 109 (including the 11 large, sexually distinct individuals) or nearly 88 per cent. of the total catch, were taken at the surface, mostly in the evening from 6 to 10 P. M., but a few as late as 4 A. M.

The remaining 16 fish were distributed so evenly between 200 and 800 fathoms that they may be accredited to casual captures, perhaps entering the nets at higher elevations than the extreme depths of the hauls indicate. The actual data are; 200 fathoms (1 fish), 300 (1), 400 (2), 500 (6), 600 (3), 700 (2), and 800 fathoms (1 fish). The fact that none were taken in daylight surface hauls suggests that there is a decided migration downward during daylight hours.

*Sociability:* Very convincing evidence is shown of schooling, since 66 specimens, representing 53 per cent. of the total 125, were taken in four nets. The details are as follows: 25 nets (1 fish each), 9 (2), 2 (3), 2 (4), 1 (6), 2 (8), 1 (16), and in 1 net (30 fish).

*Food:* Representatives of three Phyla were found in the stomachs of *Myctophum aurolaternatum*: Coelenterata, Crustacea and Mollusca.

The contents of 10 stomachs are typical of the food in general. All these fish were taken at the surface at night: Cat. No 5324

(36 mm.) 1 hyperian amphipod, 1 pycnogonid; 5539 (68 mm.) 3 amphipods; 6057 (41 mm.) 1 caridean; 6057 (37 mm.) 1 stalk-eyed shrimp, 3 amphipods, 3 copepods; 6059 (76 mm.) 4 copepods; 6061 (71 mm.) 4 isopods; 6061 (41 mm.) 1 isopod, 2 copepods; 6270 (38 mm.) 1 small squid, red eye with accessory light organs, 2 copepods; 6270 (36 mm.) 1 small squid, red eye, no light organs, 3 copepods; 6421 (75 mm.) 2 euphausiids, 2 siphonophore segments, 3 zoea.

**Luminescence and viability:** Even in the specimens taken at the surface, viability was so poor that only three fish survived transportation to the dark room from the lighted deck. In all of these the lateral AO photophores were glowing with a faint bluish radiance. From one fish, three short, very intense, pale flashes were recorded, so powerful that the entire fish, its jar and our hands were brilliantly illuminated.

**Parasites:** Four of the larger specimens, with well-developed glands, had large parasitic copepods attached to the sides, all with a pair of dangling ovaries.

#### STUDY MATERIAL.

A total of 125 specimens was taken, as follows: *Arcturus* Expedition, Station 39 T-3(1); 41 T-3(1); 45 T-5(3); 47 T-1(2); 49 T-1(1); 50 T-1(1); 52 T-1(1); 52 T-2(2); 57 T-1(2); 58 T-1(1); 59 T-8(1); 59 T-9(1); 61 Pt-1(1); 61 T-4(1); 61 T-5(1); 62 T-1(2); 65 T-4(3); 65 Ot-1 to Ot-4(8); 73 T-1(2); 74 T-26(1); 74 T-35 to T-40(16); 74 T-40(1); 74 T-41(2); 74 T-42(30); 74 T-41 and T-42(6); 74 T-43 and T-44(8); 74 T-69 to T-71(2); 74 T-70(1); 84 T-15 to T-17(4); 84 T-21(1); 86 T-4(1); 87 Pt-1(2); 88 T-2(1); 90 T-1 and T-2(1); 91 T-2(1). Templeton Crocker Expedition, Station 160 L-1(1); 161 L-1(1); 162 L-1(1). Eastern Pacific (*Zaca*) Expedition, Station 210 T-3(1); 210 L-1(2); 210 T-8(1); 228 T-1(1); 231 L-1(4). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 108).

##### *Myctophum aurolaternatum*:

Garman, 1899, p. 264, pl. IV, fig. 3. (4 large and 21 small specimens, including type; ? to 90 mm.; surface; Gulf of Panama. Description and reference to luminosity).

Parr, 1928, p. 65. (Key to species).

Parr, 1934, p. 43, fig. 2. (Examination and redescription of type specimens).

##### *Myctophum (Myctophum) aurolaternatum*:

Bolin, 1939, pp. 92, 105, 108-109, fig. 10.

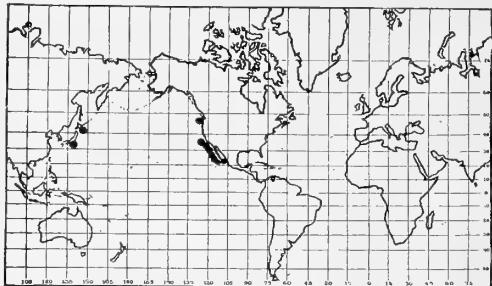
(6 specimens; 31 to 72.4 mm.; ? fathoms; Gulf of California and off Panama).

##### *Myctophum californiense* Eigenmann & Eigenmann, 1889.

**Specimens taken by Eastern Pacific Expeditions:** 5 specimens; Templeton Crocker Expedition; surface to 500 fathoms; between 23° 25' and 30° N. Lat., and 108° 31' and 116° 27' W. Long.; lengths 31 to 38 mm.; between April 29 and May 23, 1936.

8 specimens; Eastern Pacific (*Zaca*) Expedition; surface; 31° 25' N. Lat., and 116° 58' W. Long.; lengths 30 to 44 mm.; taken on Nov. 7, 1937.

**Specimens previously recorded:** 13 specimens; ? to 127 mm.; ? to 534 fathoms; both shores of the Pacific, on the east from Puget Sound to Cape Lucas, and in the west, off Japan. Material in the present paper extends the known range about 600 miles south, 48 miles east of Arena Point, Lower California.



TEXT-FIG. 4. Distribution of *Myctophum californiense*.

**Photophore variation:** There is little variation in the number of anal photophores in our 13 specimens. The commonest pattern is a symmetrical 7-9, shown by 8 specimens, or more than 60 per cent. of the fish. Eleven out of the 13 possess symmetrical patterns.

**Other data:** The 13 fish were all young, showing no trace of luminous glands. The extremes of measurements were 30 and 44 mm. One fish of 42 mm. taken at night at the surface had eaten 2 copepods and 1 mysid. Of the 13 specimens, 11 were taken with dipnets as they came to our night lights, three on May 23, 1926, and eight on November 7, 1937. The remaining two, although taken in a 500-fathom net, were probably much nearer the surface when they entered. Bolin says, "In life the luminous organs emit a pale greenish light."

#### STUDY MATERIAL.

A total of 13 specimens was taken, as follows: Templeton Crocker Expedition, Station 158 T-4(2); 174 L-1(3). Eastern Pacific (*Zaca*) Expedition, Station 176 L-1(8). For detailed trawling data, refer to *Zoologica*, Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-298 (*Zaca*).



## REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 106).

*Myctophum californiense*:

Eigenmann & Eigenmann, 1889, p. 124. (Type specimen; ? mm.; 45 fathoms; Cortez Banks).

Jordan & Evermann, 1896, p. 572. (Key and description).

Gilbert, 1913, p. 78. (3 specimens; all 127 mm.; ? fathoms; off Santa Barbara Islands).

Townsend & Nichols, 1925, p. 10. (1 specimen; ? mm.; 534 fathoms; southwest of Santa Barbara Islands).

Parr, 1928, p. 64. (Key and synonymy).

Parr, 1929, p. 10, fig. 4. (Further description of type).

Bolin, 1939, pp. 92, 106, fig. 9. (8 specimens; 24 to 103.3 mm.; ? fathoms; eastern Pacific off Central California, south to Mexico; key to species and description).

*Scopelus californiense*:

Lütken, 1892, p. 267. (Reference).

*Myctophum (Myctophum) humboldti*:

Brauer, 1906, p. 192. (Part of this description confused with *Myctophum californiense*).

*Myctophum coccoi* (Cocco, 1829).

*Specimens taken by Eastern Pacific Expeditions*: 4,460 specimens; *Arcturus* Oceanographic Expedition; surface to 1,000 fathoms; between 6° 58' N. Lat., and 2° 00' S. Lat.; and between 80° 48' and 91° 47' W. Long.; lengths 13 to 51 mm.; between April 3 and June 19, 1925.

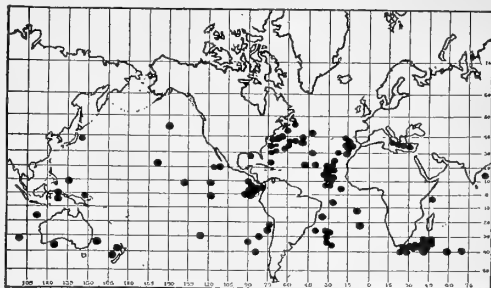
3 specimens; Templeton Crocker Expedition; surface; at 18° 44' N. Lat., and 114° 20' W. Long.; and at 21° 20' N. Lat., and 115° 14' W. Long.; lengths 20 to 29 mm.; May 9 and 17, 1936.

3 specimens; Eastern Pacific (*Zaca*) Expedition; surface; 4° 30' N. Lat., and 78° 33' W. Long.; lengths 13 to 20 mm.; March 26, 1938.

*Specimens previously recorded*: 996+ specimens; ? to 110 mm.; ? to 2,620 fathoms; in all parts of the Atlantic Ocean, north, south, east and west, as well as mid-ocean, between 40° S. Lat. and 48° N. Lat.; Mediterranean Sea, Cape of Good Hope, south of Zanzibar, Bay of Bengal, Indian Ocean, east and west of Australia, Admiralty Islands, Philippines, Japan, mid-Pacific, south-east of Hawaii, between Galápagos and Marquesas Islands, Gulf of Panama, coast of Central America, off coast of Chile.

In the eastern Pacific *Myctophum coccoi* is very evidently more at home in southerly warm waters, as witness the 4,400 specimens taken on the *Arcturus*, between Panama and the Galápagos, this number being almost half the total of all the members of

this family taken on the whole of this expedition. On the other two expeditions only 6 were taken, all at the surface at night lights. One swam into a dipnet about 50 miles north of Gorgona off the Columbia coast, and a single specimen came from well off shore at a latitude only 100 miles south of Cape Lucas, forming the northernmost Pacific record for this species. Thus 20 degrees north is the limit in the Pacific, whereas in the Atlantic, *coccoi* is found as far north as 48 degrees. Forty degrees south seems the abrupt deadline for the species all around the world. Within these latitudinal limits the fish may be said to be almost cosmopolitan.



TEXT-FIG. 5. Distribution of *Myctophum coccoi*.

*Photophore count and variation*: There is a great variation in the number of anal photophores, even in the same specimen, fish after fish having a different count on either side. This has nothing to do with sex or age. A count of the anal photophores on more than 200 specimens, reveals that the most common combination (76 specimens) is 6-11. The next most common is 6-10. To summarize, there are six combinations in 136 fish, 35 combinations in 73 fish, or a total of 41 separate combinations in 209 fish.

Previous studies on about 1,500 freshly caught fish resulted in their division into dominant variants from the standard numbers of anal photophores, there being eight distinct types in addition to the more normal ones.

*Types of variations other than Numerical, in Anal Photophore Groupings.*

1. No break between anterior and posterior groups, one side only.

2. No break between the posterior group and the precaudal photophores.

3. Anterior group divided between second and third photophores.

4. Anterior group irregular in spacing because of the apparent insertion of an extra photophore.

5. One photophore in series out of line with the rest.

6. Break in either group or in the precaudals.

7. Three precaudals instead of two, on one or on both sides.

8. Smaller photophores in the series.

The extent of the eight variants in 1,104 individuals is unexpectedly great. Including males, females and older young, 57.8 per cent. possess the normal complement and arrangement of anal photophores, while those fish showing one, two or three of the variations comprise the remaining 42.2 per cent.

*Luminous glands:* As in nearly related species, the presence of supracaudal glands indicate male fish more or less adult, while the female is associated with infracaudal glands. Ontological development is shown by the following 70 fish, 37 of which were males, and 33 females.

Males of 34 to 40 mm. average 4.4 glands; those of 40 to 45 mm. 4.4 glands; males 45 to 50 mm. 5.2 glands. Females of 34 to 40 mm. possess an average number of 3 glands; those 40 to 45 mm. 3.5 glands; those of 45 to 50 show 4 glands. This indicates a slow but certain increase in number of glands with increase in standard length.

*Sex proportions:* Eleven hundred and four *M. coccoi* were taken at two *Arcturus* stations in the Pacific, Station 39, T-1; and 84, T-15 T-16 and T-17). This number comprised 24.7 per cent. of the entire Pacific catch of this species. Of these 1,104 fish, 619 were young, 253 males and 232 females. In a few other small catches the females actually equalled the numbers of the males, so that occasionally the balance is quite even between the sexes. The total count of all 4,466 Pacific *M. coccoi* resolves into 45.7 per cent. young, 30.6 per cent. males, and 23.7 per cent. females.

*Breeding:* A full grown female of 50 mm. length, taken at the surface off the Galápagos on April 12, had ovaries 9 mm. in length. The egg diameters were .25 mm. and the total count of the eggs in one ovary was 1,648, or about 3,300 eggs altogether.

*Vertical distribution and migration:* The number of *M. coccoi* taken below the surface is negligible, except in the case of a single net drawn at a depth of 200 fathoms, in the evening, from 7.40 to 8.35 P. M. and which contained 42 fish. Deeper hauls averaged 300 fathoms (4 fish), 400 (2 fish), 500 to 1,000 fathoms (1 fish each). The total of sub-surface fish is 59 as compared with 4,407 from the surface. Doubtless the great majority, if not all, of the 17 individuals from below 200 fathoms were adventitious, probably entering at or near the surface during the brief passage of the net at the upper levels.

The daily migration is evident from the following table, giving the number of fish drawn at successive half hours. A. M. hauls were actually consecutive.

HOUR		No. OF FISH
A. M.	12.00-12.30	39
	1.00- 1.30	26
	2.00- 2.30	25
	3.00- 3.30	10
	4.00- 4.30	10
	4.30- 5.00	13
	6.00- 6.30	2
(No fish taken between 6.30 A.M. and 6.30 P.M.).		
P. M.	6.30- 7.00	5
	7.00- 7.30	63
	7.30- 8.00	113
	8.00- 8.30	186
	9.00- 9.30	145
	9.30-10.00	88

This sequence was confirmed by several Station series well removed from one another. At Station 74 I made half-hour hauls around the clock, and again fifteen-minute hauls at 5 to 7 o'clock both morning and evening, to confirm the regularity of appearance and disappearance. This slender-tailed lantern fish comes up from rather shallow depths just after dark on the equator and rapidly reaches its greatest abundance, or perhaps at this time, 8-9.30 P. M., keeps in very dense, compact schools. Throughout the night its numbers in the nets decrease, probably from a general scattering in search of food, and the last individual dives into darker levels at 6.30 A. M. at the very latest. Judging from the contents of our nets, the younger fish appear at the surface first, and seem to vanish sooner than the older ones, but this last statement is less certain because of the suddenness with which all descend.

Rough water seems to deter them but little in their vertical movements, but a much more potent factor is the presence or absence of moonlight. On a cloudy night a half hour tow brought in 40 fish, while on the following night, in clear, nearly full moonlight, a similar net at a corresponding hour captured only two. Fifteen additional instances all provided identical data.

Only rarely have I observed this lantern fish in its native element. At the foot of the companionway with an electric light cluster swung low over the water, on three occasions I have observed this species, and twice captured it. I can account for this unexpected positive phototropism only by a reversal of reaction due to some factor in the greater intensity and concentration of the illumination.

As my nightly tows show, *coccoi* is present in large numbers at the surface of a wide area of the Pacific. Whenever many individuals have been taken in one net, the variation in age has been great, very young and fully developed adults being mingled together. In general shape and in the remarkably nondeciduous scales *coccoi* differs greatly from its generic relations.

**Sociability:** While the summation of catches presents a uniform and logical picture of vertical distribution, migration and sociability, irregularities are now and then apparent. For example, two nets at Station 39, T-1 and T-2 drawn simultaneously, parallel, but from different sides of the stern, in a half hour's time caught respectively 4 and 72 fish, illustrating the concentration of schooling in certain places and at definite times. A third net attached ten minutes after the other two, captured 600 *M. coccoi* in thirty minutes.

The record for numbers in a short period of time was at Station 88, on the equator in the Galápagos, when four small nets, one-half metres, were pulled from 8.10 to 9.00 P. M.; 9.00 to 9.30; 9.35 to 9.40 and 9.45 to 9.50. The count of *M. coccoi* was 293, 315, 116 and 549. The last two hauls of five minutes each thus captured more than 66 fish a minute, and this in nets only 18 inches in diameter. The 1,273 *coccoi* here taken in a little more than an hour and a half, represent almost one-third of the entire catch on the *Arcturus* in the Pacific.

If we assume that 40 or more *coccoi* taken in a single net constitute evidence of schooling, then we find that out of 52 nets pulled on the surface, 25 come within our assumption. These include captures of 40 to 600 individuals, in all 4,147 fish, or about 92 per cent. of the entire catch, an average of 165 *coccoi* to each net.

**Food:** The slender-tailed lanternfish is altogether a plankton feeder. In the beginning of our deep sea work, my assistants several times brought me individual fish which had partly ingested the entire head of a fellow *M. coccoi*. This astonishing sight was subsequently observed a number of times, and proved to be wholly accidental. The newly caught fish, gasping and gaping widely, wriggling about at full speed in a small aquarium, sooner or later ran against and partly engulfed the head of a smaller fish.

A haul at the surface on June fifth, near the Galápagos, at Station 78, T-1, yielded 40 *Myctophum coccoi*. These were all examined at once for the contents of their stomachs with the following results:

1. 3 small calanids, 5 hyperids, 3 *Corycaeus*, 1 euphausiid.
2. 12 calanids, 3 hyperids, 1 *Halobatis*, 1 small *Atlanta*.
3. 1 calanid, 5 hyperids, 1 *Atlanta*, 1 *Pontella*.
4. 21 calanids, 1 *Candace*, 1 *Monops*, 1 *Pontella*, 1 *Sapphirina*, 3 hyperids, 1 euphausiid, 1 *Atlanta*, 1 *Limacina*.
5. 15 calanids, 1 *Corycaeus*, 5 hyperids, 1 *Monops*, 1 *Limacina*.
6. 18 calanids, 3 hyperids, 1 mysid, 1 fish egg, 1 *Globigerina*.

7. 22 calanids, 4 hyperids, 3 *Atlanta*, 3 *Globigerina*, 1 *Limacina*.
8. 2 *Monops*, 1 schizopod, 1 fish egg, 13 calanids, 1 *Sagitta*.
9. 9 hyperids, 21 calanids, 25 *Limacina*, 1 *Atlanta*, 1 *Monops*.
10. 8 calanids, 3 hyperids.
11. 9 calanids, 6 hyperids, 2 *Limacina*, 3 *Sagitta*, 3 *Globigerina*.
12. 14 calanids, 4 hyperids, 2 *Sagitta*.
13. 7 calanids.
14. 8 calanids, other material.
15. 2 hyperids, 5 *Sagitta*, 2 *Corycaeus*.
16. 1 hyperid.
17. 3 *Sagitta*, 4 calanids, 1 hyperid, 5 fish eggs.
18. 1 hyperid, 1 euphausiid, 8 calanids, 4 *Limacina*, 1 ostracod.
19. 7 hyperids, 1 *Monops*, 2 fish eggs, 1 *Globigerina*.
20. 8 hyperids, 1 *Ianthina*, 2 fish eggs, 1 *Limacina*.
21. 2 hyperids, 1 euphausiid, 3 calanids.
22. 2 *Candace*, 3 fish eggs, 6 hyperids.
23. 3 small mollusks, 2 hyperids, 2 small worms.
24. 14 *Candace*, 2 hyperids.

25 to 40. Fifteen stomachs empty or with unrecognizable material.

The general aspect of this food of *M. coccoi* resolves into the following:

	No. TIMES EATEN	No. INDIVIDUALS
Annelids	2	2
<i>Atlanta</i>	5	7
Calanids	17	183
<i>Corycaeus</i>	2	5
Euphausiids	4	4
Fish eggs	7	15
Gastropods	1	3
<i>Globigerina</i>	5	9
<i>Halobatis</i>	1	1
Hyperids	21	80
<i>Ianthina</i>	1	1
<i>Limacina</i>	6	34
<i>Monops</i>	4	5
Mysids	2	2
Ostracods	1	1
<i>Pontella</i>	3	3
<i>Sagitta</i>	5	14
<i>Sapphirina</i>	1	1
Schizopods	1	1
	89	371

Carrying this finally to groups, we find that fish eggs have entered 7 times into the diet; insects once; mollusks 13 times, crustaceans 55 times; annelids 77 times and protozoans 5 times.

**Viability:** Roughness of water seems to make very little difference to this fish, and on nights when the sea was rough and the

swell heavy, I have still taken them in abundance. At such times other species of myctophids have remained below, perhaps in part due to the delicacy of attachment of their scales. *Coccoi* can stand an astonishing amount of buffeting and handling without the loss of a single scale.

Viability is another quality which sets *coccoi* apart. A net full of mixed surface fish will always have living *coccoi* after all the others have died. Not only this, but there is marked individuality within the species. One fish which we named "Methusalem" lived on and on after I had subjected him to all sorts of experiments, dropped him on the floor twice, and placed him for a moment by mistake in a bowl of formalin.

The moment a slender-tailed lanternfish is removed from the tow net and placed in a container of clear salt water, he begins swimming violently and ceases activity only with death. Other myctophids sometimes rest or relax somewhat their violent efforts at escape, but *coccoi* never. The contour of the body, slender and compressed anteriorly and drawn out into an elongated narrow posterior, compels a wholly different method of progression from that of its stouter, more rounded relatives. There is no steady or slightly undulatory movement, but a violent wagging of the entire body and tail, such as is seen in small elvers and muraenoids. In a still living lanternfish the tail can be bent around more than 360 degrees from the anterior portion of the body and tail, forming more than a complete circle. Much of this entire flexibility is apparently utilized at each progressive effort.

As in the case of many other deep-sea fish, the first instinct on being exposed to light, is to descend. This is the case both in shallow dishes and in deep aquaria. The fish makes one straight dive to the bottom, and from then on gyrates head downward, twisting and pushing, endeavoring to achieve the only known method of escape. From this and other facts, it seems certain that danger threatens these small beings almost altogether from above. Once when a short haul had provided some unusually virile, active lanternfish, by placing several immediately in an aquarium of running water, I managed to have one remain at the surface. It swam obliquely with the head at the very surface, and around and around rapidly, wriggling violently and covering every inch of the water. Furthermore, when the lights were turned out in the aquarium room, a large individual which had been bumping its head off against the bottom, suddenly veered upward, and wiggled to the surface, to dash about for a minute like its fellows. A sudden glare of light sent them both down to a few minutes more of gyration and then death.

Unexpectedly and with no cessation of

the frantic wriggling movements I have seen fish at several different times, turn, seize and swallow small forms of plankton life which swam close to them, this in diffused room light plus the ventral sheet of luminescence.

*Luminescence:* The abundance and the unusual viability of *Myctophum coccoi* made possible the observation of these fish in the dark room of the *Arcturus*. Imagine a minnow which is iridescent copper above and silvery white below, not over two inches in length, with large eyes and moderate fins. A full-grown fish weighs a gram, which means that it would take about 450 to make a pound. It feeds on copepods, amphipods, floating snails and other minute plankton fry, and from this food it generates sufficient energy to swim, to make daily migrations up and down, to illumine one hundred lights and to deposit upwards of two to three thousand eggs.

Scattered over the body are many, small, round luminous organs, which we may divide into three general sets. First, 32 ventral lights on each side of the body, extending from the tip of the lower jaw to the base of the tail; second, about 12 lateral lights arranged irregularly along the head and body, and third, a series of three to six median light plates or scales, either above or below the base of the tail.

The lower battery, when going full blast, casts a solid sheet of light downward, so strong that the individual organs could not be detected. Five separate times when I got fish in a large, darkened aquarium, I saw good-sized copepods and other organisms come close, within range of the ventral light, then turn and swim still closer to the fish, whereupon the myctophid twisted around and seized several of the small beings. Once it turned completely on its back. I could never have seen this except that the glass sides reflected sufficient light. Whether this is the chief object of the ventral lighting I do not know, but it was at least effective on the several occasions when I was watching.

Perhaps the best distinction between various species of lanternfish is the arrangement of the lateral light organs, and in the darkroom in absolute darkness I could tell at a glance what and how many of each species were represented in a new catch, solely from their luminous hieroglyphics. When several fish were swimming about, these side port-holes were almost always alight, and it seems reasonable that they may serve as recognition signs, enabling members of a school to keep together, and to show stray individuals the way to safety.

The light scales of the tail are apparently of considerable importance. Ordinarily when the whole fish is glowing with the pale greenish light of luminescence, these caudal

lights are seldom seen. A clue to their use is found in the fact that they show a sexual difference, the males having them on the upper side of the peduncle and the females on the lower side. In my brief and sporadic observations, when no fish lived longer than thirty-six hours, there was no chance to watch signs of courtship or any such use which these lights might subserve. But when a fish exerted itself unduly to get out of the way of another, either of its own or another species, these lights would flash and die in quick succession. Three separate times in unusually strong, vigorous fish when the body luminescence was very dim, these scale searchlights flashed like heliographs, being much stronger than the combined, steadier glow of all the others. This luminescence was of a much deeper green than that of the ventral lights. If continuously alight, a single fish would have illumined the whole darkroom, and enabled one easily to read fine print.

In the dark it was thus possible to distinguish species of lanternfish by the lateral hieroglyphics and the sexes by the upward or downward direction of the tail lights. I have never seen the latter illumination given out by a fish swimming alone in an aquarium. Although it is very evident that the caudal flashes have some sexual significance, yet another very important function seems that of obliteration. It certainly was to my eyes and I have no reason to think that a natatory enemy might not also be frustrated. When the ventral lights die out they do so gradually, so that the eye holds the image of the fish for a time after their disappearance, but the eye is so blinded by the sudden flare of the tail lights that when they are as instantly quenched, there follow several seconds when our retina can make no use of the faint, diffused, remaining light, but becomes quite blinded. A better method of defense and escape would be difficult to imagine.

Specimens of *Myctophum coccoi* taken around midnight seemed to show less brilliant light and more intense color, a deeper turquoise green than those captured earlier. It seems possible that the color varies inversely in strength with increase of luminescence (at least in its effect on the human eye), that is, the more powerful the actual luminescence, the more it obscures the specific color. In lighted surroundings the luminous activity is minimized, and the color at maximum, while as the luminescence increases in intensity the color shows up less. To repeat, specimens taken under the above conditions show the color very well, whereas the luminescence was not as intense as that in fish caught at the surface soon after dark. This was observed independently by several of us again and again and seems to indicate a certain

relative independence of light intensity and color functioning.

*Enemies:* While the number of the enemies of myctophids must be legion there is one which seems to consider these small fish as an almost exclusive item of diet. Not long after the first of the *coccoi* come to the surface, a somewhat larger, black fish is to be found in the same nets. In the glare of the laboratory lights this was not a very unusual appearing fish, although it had a short, dependent chin tentacle and a mouth with exceedingly wide gape. Its name is *Astronesthes*. Almost every specimen taken of this fish contained a recently swallowed *coccoi*, usually measuring about two-thirds the length of its enemy. In the dark, *Astronesthes* itself is a gorgeous sight, the skin covered with a host of minute luminous specks, while the fins fairly glowed with pale green light. Strangely enough, the stem only of the tentacle was luminescent, while the slightly enlarged tip was dark.

*Parasites:* *Myctophum coccoi* appears to be more susceptible to parasitic infection than is the case with other species of myctophids. For example, in a female 35 mm. in length, (Cat. No. 6397), three parasites were found in the body cavity; a larval cestode of the genus *Rhyncobothrium*, lying free in the left side between an ovary and the intestine. It measured 7 by 2.2 by .62 mm. and was transparent enough to show the proboscides. On the right side of the body cavity a 7 mm. larval acanthocephalid was situated slightly above and partly inside the pancreas. In front of the liver, between it and the pigmented peritoneal lining and just below the oesophagus, partly coiled around it, was an immature nematode, a 6 mm. *Anisakis*.

#### STUDY MATERIAL.

A total of 4,446 specimens was taken, as follows:

*Arcturus* Expedition, Station 33 T-1(1); 33 Pt1(1); 33 T-2(58); 38 Pt-2(2); 38 T-1(8); 39 T-1(4); 39 T-2(71); 39 T-2(1); 39 T-3(70); 39 T-3(529); 39 T-3(1); 39 T-5(87); 40 T-1(2); 41 T-1(2); 41 T-3(135); 45 T-1(29); 45 T-1(1); 47 T-1(44); 47 T-1(27); 47 T-1(12); 47 T-1(2); 47 T-1(61); 49 T-1(42); 50 T-1(1); 50 T-5(105); 52 T-1(6); 52 T-2(24); 53 T-3(2); 57 T-1(424); 58 T-1(5); 62 T-1(2); 63 T-1(3); 65 T-1(2); 65 T-3(2); 65 T-4(10); 65 surface(10); 67 T-1(2); 68 T-1(4); 68 T-5(1); 70 T-1(3); 73 T-1(5); 74 T-10(6); 74 T-11(20); 74 T-23(94); 74 T-26(39); 74 T-29(43); 74 T-35(2); 74 T-35 to T-40(78); 74 T-41(24); 74 T-43 and T-44(18); 74 T-46(13); 74 T-61 to T-66(50); 74 T-70(1); 77 T-1(17); 84 T-2(2); 84 T-5(41); 84 T-6(2); 84 T-8(3); 84 T-14(1); 84 T-15 to T-17(223); 84 T-16(282); 84 T-20(2); 85 T-1(103); 86 T-5(1); 86

T-8(1); 88 T-1 and T-2 to T-4(49); 88 T-1(274); 88 T-2(296); 88 T-3(116); 88 T-4(512); 90 T-1 and T-2 (163); 91 T-1(174); 91 T-1(2); 91 T-2(16). Templeton Crocker Expedition, Station 162 L-1(2); 167 L-1(1). Eastern Pacific (*Zaca*) Expedition, Station 231 L-1(3). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-289 (*Zaca*).

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1928, p. 61).

##### *Scopelus coccoi*:

Cocco, 1829, p. 143. (Reference not seen).  
Cocco, 1838, p. ?, pl. II, fig. 6. (Reference not seen).

Bonaparte, 1832-41, p. 138. (Description).  
Cuvier & Valenciennes, 1828-49, vol. 22, p. 440. (Brief description; 1 specimen; no details).

Günther, 1864, vol. 5, p. 413. (Description; ? specimens; ? mm.; ? fathoms; Gulf of Guinea, Mediterranean and Atlantic).

Günther, 1889, vol. 31, p. 30. (Description; 80 specimens; ? mm.; ? fathoms; south of Cape Verde, near West Indies, south Atlantic, south Pacific, mid-Pacific, near Admiralty Islands and near Japan).

Canestrini, 1870, p. 125. (Reference not seen).

Doderlein, 1878-79, p. 54. (Name listed only).

Raffaele, 1889, p. 182, pl. 7, fig. 5. (Description).

Moreau, 1891, p. 90. (Description).

Collet, 1896, p. 116. (Description; synonymy; 42 specimens; ? mm.; surface; Azores and south of Flores).

Gilchrist, 1908, p. 165. (150 specimens; ? mm.; surface; Cape Point, South Africa).

Thompson, 1916, p. 83. (Name listed, with synonymy).

##### *Scopelus gracilis*:

Lütken, 1892, p. 255, fig. 13. (Description; 5 specimens; ? to 50 mm.; ? fathoms; open Atlantic near Madeira, mid-north Atlantic, off Cape of Good Hope, south of Zanzibar, off coast of Brazil).

##### *Scopelus jagorii*:

Peters, 1859, p. 411. (Reference not seen).

##### *Scopelus langerhansi*:

Johnson, 1890, p. 454. (1 specimen; 110 mm.; ? fathoms; Madeira).

Lütken, 1892, p. 267. (Reference only).

##### *Scopelus (Rhinoscopelus) coccoi*:

Lütken, 1892a, p. 243. (? specimens; ? to 50 mm.; ? fathoms; large number of stations, both east and west, north and south Atlantic, east and west of Australia,

south Africa, Zanzibar. All recorded on distribution map).

Carus, 1889-1893, p. 564. (Description).  
*Rhinoscopelus coccoi*:

Goode & Bean, 1895, p. 90. (Brief description; ? specimens; ? mm.; surface to 2,620 fathoms; northwest Atlantic from Newfoundland to Gulf of Mexico, Bermuda, Madeira).

Jordan & Evermann, 1896, p. 568. (Description).

Fowler, 1928, p. 70, fig. 14. (References; synonymy; brief description).

##### *Rhinoscopelus tenuiculus*:

Gilbert, 1908, p. 222. (Brief description; 1 specimen; 50 mm.; ? fathoms; southeast of Hawaii).

Gilbert, 1911, p. 15. (Brief description; 12 specimens; 35 to 50 mm.; ? fathoms; midway between Galápagos and Marquesas Islands).

Jordan & Jordan, 1925, p. 11. (Name listed only).

##### *Alysia loricata*:

Lowe, 1839, p. 87. (Brief description).

Lowe, 1849, p. 14. (Brief description).

##### *Myctophum coruscans*:

Richardson, 1844-48, vol. 2, p. 40, pl. 27, figs. 1-5. (Description; 1 specimen; 57 mm.; ? fathoms; south Atlantic, Australia).

##### *Scopelus coruscans*:

Hutton, 1873, p. 270. (Brief description).

##### *Myctophum hians*:

Richardson, 1844-48, vol. 2, p. 41, pl. 27, figs. 19-21. (Description; 1 specimen; 50 mm.; ? fathoms; ? locality).

##### *M. (Myctophum) hians*:

Brauer, 1906, pp. 162, 194, fig. 12. (Key to species; description; synonymy; 1 specimen; 22 mm.; 1,903 fathoms; south Atlantic).

Barnard, 1925, p. 244. (Brief description).

##### *Myctophum tenuiculum*:

Garman, 1899, p. 262, pl. J, fig. 5. (Description; 1 specimen; 25 mm.; surface; Gulf of Panama).

##### *Myctophum gracile*:

Goode & Bean, 1895, p. 74. (Brief description).

Jordan & Evermann, 1896, p. 572. (Brief description).

##### *Myctophum (Rhinoscopelus) coccoi*:

Roule & Angel, 1933, p. 28. (1 specimen; 53 mm.; surface; Azores).

##### *M. (Myctophum) coccoi*:

Brauer, 1906, pp. 163, 199, figs. 116-120. (Key to species; description; synonymy; 380 specimens; ? to 52 mm.; between Azores and Newfoundland, north of Bermuda, West Indies, north of Bahamas, Gulf of Mexico,



south Atlantic, coast of Brazil, Madeira and Canary Islands, Cape Verde, Gulf of Guinea, Indian Ocean, Zanzibar, Admiralty Islands, East Indies).

Pappenheim, 1914, p. 194. (93 specimens; 20 to 46 mm.; ? to 1,642 fathoms; south Atlantic, Cape Verde).

Barnard 1925, p. 244. (Brief description).

*Myctophum coccoi*:

Weber & Beaufort, 1913, pp. 153, 158. (Key to species description; synonymy).

Regan, 1916, p. 134. (Description of larval and postlarval fishes of New Zealand and 3 Kings Island; 1 specimen; 20 mm.; 2 fathoms).

Sanzo, 1918a, p. 135. (Description of young).

Tåning, 1918, pp. 67-70, figs. 23, 24. (Detailed description of adult and postlarval fish; distribution map; 64 specimens; 5 to 34 mm.; surface to ? fathoms; eastern Mediterranean).

Tåning, 1928, p. 55. (Key to species).

Tåning, 1932, p. 113, figs. 1, 2. (Description of adults and postlarval; synonymy).

Barnard, 1925, p. 236. (Key to species).

Parr, 1928, p. 61. (Key to species and synonymy).

Parr, 1934, p. 45. (Brief discussion).

LeGendre, 1934, p. 337. (Key to species).

Beebe, 1937, p. 204. (Preliminary list; 165 specimens; 7 to 26 mm.; 300 to 1,000 fathoms; Bermuda).

*Myctophum evermanni* Gilbert, 1905.

*Specimens taken by Eastern Pacific Expeditions*: 105 specimens; *Arcturus* Oceanographic Expedition; surface to 1,000 fathoms; between 6° 40' N. Lat., and 0° 03' S. Lat., and 80° 49' and 89° 50' W. Long.; lengths 18 to 73 mm.; between Feb. 23 and July 29, 1925.

3 specimens; Eastern Pacific (*Zaca*) Expedition; 1 at 300 and 2 at 500 fathoms; between 9° 09' and 8° 03' N. Lat., and 83° 12' and 85° 04' W. Long.; lengths, 16, 16 and 18 mm.; Feb. 8 and March 10, 1938.

Of these myctophids 80 have been available for study.

*Specimens previously recorded*: 41 speci-

mens; surface to 1,100 fathoms; Hawaii, Marquesas, East Indies and Japan. Our specimens are the first recorded from the eastern Pacific.

*Photophore variation*: Unlike other species of this genus the lateral photophores show no bilateral asymmetry. The pattern of 8-5, 8-5 is the most common, comprising 61 per cent. of the whole. The extremes are 7-5 and 8-6.

*Luminous glands*: Of 80 specimens, 44, from 16 to 31 mm. show no signs of caudal plates. Seventeen males, 40 to 69 mm. present 6 to 8 supracaudal plates. There is a decided increase in number with size, i.e., 6 fish with 6 plates average 48 mm.; 10 with 7 plates average 57 mm. and 1 fish with 8 plates is 56 mm. in length.

Nineteen are females and starting with a single plate faintly visible in a 43 mm. specimen, the series ends with four well-developed plates and a length of 73 mm. The corresponding series of lengths in the ascending plate scale is 45, 52, 53, 61, 61 and 67 mm.

*Breeding*: Specimen No. 6059, 68 mm. in length, taken June 1, is a female in full breeding condition with ovaries measuring 28 by 5.5 mm.

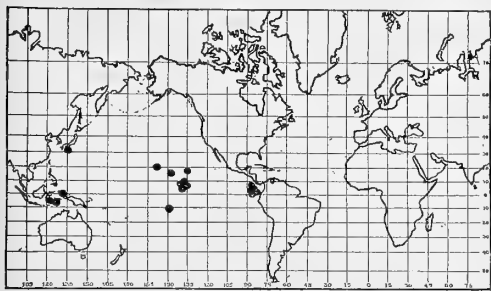
*Vertical distribution*: Eighty-five per cent. of the total catch was taken at the surface, all after dark. The 12 specimens brought up from open nets descending to 300 and 600 fathoms are so evenly distributed that they may well have entered at considerably more shallow depths. All 36 recognizable males and females were taken at the surface.

*Sociability*: Schooling, especially of older fish, is definitely shown from the fact that 43 of the 80 (including all the sexually recognizable specimens) comprising 54 per cent. of the whole, were taken in three hauls at the surface at night, while the remainder averaged one and one-half fish to the net. In one haul of 10 young fish, all were of exactly the same age, 22 mm. in length.

*Food*: In ten stomachs there were remains of three phyla; Crustacea, Mollusca and Pisces. The following groups were present in this order of abundance; copepods, 44 individuals of at least six species; 29 amphipods; 13 pteropods of three species; 13 cuphausids; 4 schizopods; 3 larval fish; 2 shrimp.

#### STUDY MATERIAL.

A total of 84 specimens was taken, as follows: *Arcturus* Expedition, Station 29 surface(1); 31 surface(1); 47 T-1(10); 59 T-9(3); 65 T-3(1); 65 T-4(2); 65 T-4(1); 66 T-2(3); 66 T-2(1); 67 T-1(1); 68 T-5(1); 73 T-1(4); 74 T-4(1); 74 Pt-2(1); 74 T-10(1); 74 T-10(1); 74 T-11(1); 74 T-15(1); 74 T-24(3); 74



TEXT-FIG. 6. Distribution of *Myctophum evermanni*.

T-26(2); 74 T-29(1); 74 T-35(0); 74 T-42(10); 74 T-43(23); 74 T-61(3); 74 T-74(1); 90 T-1(1); 91 T-2(2). Eastern Pacific (*Zaca*) Expedition, Station 210 T-7(2); 219 T-2(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES AND SYNONYMY.

##### *Myctophum evermanni*:

Gilbert, 1905, p. 597, pl. 70, fig. 2. (Holotype; 29 mm.; surface; south of Oahu, Hawaii).

Gilbert, 1908, p. 218. (11 specimens; ? mm.; ? fathoms; 1,300 to 1,500 miles south-east of Hawaii and to Marquesas).

Gilbert, 1913, p. 80. (15 specimens; ? mm.; surface; off southeast Japan).

Brauer, 1906, p. 162. (Key to species).

Weber, 1913, pp. 86, 87. (4 specimens; 20 to 48 mm.; ?—550 to 1,100 fathoms; East Indies).

Weber & Beaufort, 1913, p. 162, fig. 63. (Description and figure).

Jordan & Jordan, 1922, p. 11 (Name listed).

Fowler, 1928, p. 70. (10 specimens; ? mm.; ? fathoms; Hawaii).

Parr, 1928, p. 65. (Key to species).

Parr, 1929, p. 10. (Reexamination of type specimen, and considers it adequately described and figured by Gilbert).

Norman, 1929, p. 514. (1 specimen in British Museum, identified by Günther as *M. caninianum*, reexamined and referred to *M. evermanni*; ? mm.).

##### *Myctophum laternatum* Garman, 1899.

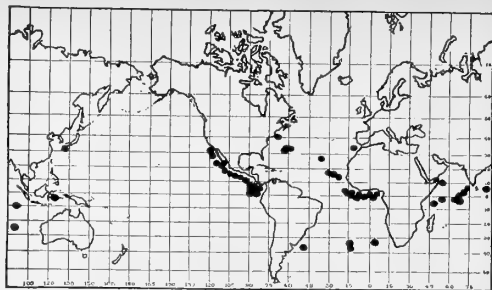
*Specimens taken by Eastern Pacific Expeditions*: 617 specimens; *Arcturus* Oceanographic Expedition; surface to 1,200 fathoms; between 2° 00' S. and 6° 27' N. Lat., and 81° 08' and 91° 53' W. Long.; lengths 8 to 28 mm.; between April 13 and June 13, 1925.

129 specimens; Templeton Crocker Expedition; 300 to 550 fathoms; between 20° 36' and 26° 48' N. Lat. and 108° 31' and 113° 25' W. Long.; lengths 5 to 27 mm.; between March 28 and April 29, 1936.

425 specimens; Eastern Pacific (*Zaca*) Expedition; 300 to 500 fathoms; between 5° 10' and 17° 45' N. Lat., and 78° 42' and 103° 05' W. Long.; lengths 5 to 28 mm.; between Nov. 23, 1937 and March 26, 1938.

*Specimens previously recorded*: 2,973 specimens; surface to ca. 2,734 fathoms; north and south Atlantic Oceans, Indian Ocean, Japan and East Indies, eastern Pacific from San Diego to Galápagos.

*Photophore variation*: This species shows very general bilateral symmetry in the distribution of anal photophores, only four out of 75 fish possessing different numbers on



TEXT-FIG. 7. Distribution of *Myctophum laternatum*.

the two sides of the body. The dominant pattern is 6-3 (41 fish or 54.5 per cent.), and a second node at 7-3 (16 fish or 21 per cent.). The extremes are 5-3 and 8-3. As these last are exhibited by full-sized fish (26 mm.) and by young ones (14 mm.) respectively, it will be apparent that age has nothing to do with relative numbers of photophores.

*Luminous glands*: One hundred and seventy fish selected at random from the entire catch were examined for luminous glands. This lot of fish resolved into 87 males and 35 females, the remaining 48 being juvenile, glandless fish. The antorbital photophore is a reliable sex differentiation character, the older males having it large and well-developed, while in the females it is somewhat smaller.

In the juvenile group, from 8 to 14 mm. no trace of glands was visible. In the males, from 17 to 20 mm. the gland is of medium extent, (1.5 to 1.7 mm. in a 17 mm. fish). In large males of 20 to 28 mm., the gland is elongate (averaging 2.5 mm. in a 25 mm. fish).

*Sex proportions*: If the above mentioned proportion of the sexes holds good among larger numbers, it means the females stand in the proportion of only two-fifths of the number of males.

*Breeding*: Four breeding females, Nos. 5642, 5671, 5718 and 5719, taken from May 11 to 25 off Cocos Island, eastern Pacific, average 25.5 mm. in length. The diameter of the eggs is .45 mm. and the average length of the ovaries is 6.5 mm. The number of eggs in each ovary vary from 181 to 210, approximately 400 eggs ready to be deposited in each female.

*Vertical distribution*: *M. laternatum* is peculiar in our hauls in that there is no sharp demarcation of vertical limits, no special emphasis on certain depths. The average fish per net is as follows: surface (14 fish per net), 300 fathoms (13), 400 (9), 500 (16), 600 (10), 800 (26), 1,000 (18), and 1,200 fathoms (15 fish per net).

*Sociability*: Twenty nets contained only a single fish each, but in 14 there were from



21 to 99. The average of these was 43 fish per net. The 602 fish in these 14 nets represent more than 50 per cent. of the whole, so the evidence for schooling is reasonably positive. The depths at which these larger numbers were taken are as follows: 300 fathoms (2 nets), 450 (1), 500 (8), and 600 fathoms (3 nets).

#### STUDY MATERIAL.

A total of 1,171 specimens was taken, as follows: *Arcturus* Expedition, Station 26 surface(1); 26 T-3(1); 33 Pt-1(1); 37 surface(4); 38 Pt-2(1); 39 T-4(12); 50 T-2(3); 50 T-3(13); 50 T-4(42); 59 T-3(10); 59 T-4(6); 59 T-5(5); 59 T-8(8); 59 T-9(2); 59 T-10(10); 59 Pt-1(1); 61 Pt-1(1); 61 T-3(11); 61 T-4(9); 63 T-1(7); 66 T-2(24); 66 T-3(12); 67 T-1(14); 68 T-3(45); 68 T-5(25); 68 Pt-1(28); 74 T-1(7); 74 T-3(2); 74 T-4(8); 74 T-5(9); 74 T-7(3); 74 T-9(8); 74 T-18(5); 74 T-20(6); 74 T-21(10); 74 T-21(6); 74 T-74(26); 74 Pt-1(3); 74 Pt-3(15); 74 V-2(14); 84 T-2(11); 84 T-3(1); 84 T-6(5); 84 T-7(3); 84 T-10(7); 84 T-19(8); 84 T-20(19); 84 T-21(3); 84 Pt-1(3); 84 Pt-4(1); 86 T-2(50); 86 T-5(15); 86 T-7(2); 86 T-8(7); 86 T-9(4); 86 T-10(2); 86 T-11(10); 86 Pt-1(5); 87 T-3(24); 87 T-5(17); 87 Pt-1(1). Templeton Crocker Expedition, Station 130 T-1(11); 134 T-3(1); 148 T-2(1); 148 T-3(1); 148 T-6(3); 158 T-2(14); 158 T-3(12); 158 T-4(3); 159 T-1(8); 159 T-2(2); 159 T-3(68); 165 T-3(5). Eastern Pacific (*Zaca*) Expedition, Station 185 T-1(7); 185 T-2(4); 185 T-3(1); 210 T-1(99); 210 T-2(16); 210 T-3(7); 210 T-6(62); 210 T-7(79); 210 T-8(12); 210 T-10(22); 219 T-1(51); 219 T-2(17); 227 T-1(21); 230 T-1(27). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1928, p. 61).

#### *Myctophum laternatum*:

Garman, 1899, p. 267, pl. LVI, fig. 1. (7 specimens, including type; ? mm.; 200 to 1,168 fathoms; Gulf of California, 800 miles west of Costa-Rica, Gulf of Panama).

Gilbert, 1913, p. 77. (4 specimens; ? to 20 mm.; 300 fathoms; Japan; *partim* Bolin's *Diogenichthys scofieldi*).

Weber, 1913, p. 86. (2 specimens; 11 mm.; ? to 821 fathoms; Banda Sea north of Australia).

Weber & Beaufort, 1913, p. 156. (Description).

Regan, 1916, pp. 135, 139. (1 specimen; 8 mm.; surface; south Atlantic).

Tåning, 1918, p. 150, fig. 46. (Description of postlarval fish; 5 specimens; 5 to 20.3 mm.; ? to 875 fathoms; west of Tangiers).

Parr, 1928, pp. 61, 67. (Key to species; synonymy; discussion re *M. laternatum atlanticum*; 2 small specimens; 5,000 feet wire; near Bermuda).

Parr, 1931, p. 23, fig. 8. (2 specimens; ? mm.; 300 to 625 fathoms; cable; off west coast Mexico).

Parr, 1934, p. 42, fig. 1. (Examination and description of type specimens).

Norman, 1930, p. 324. (15 specimens; 11 to 27 mm.; ? to 1,368 fathoms; south Atlantic).

Roule & Angel, 1930, p. 48. (1 specimen; 16 mm.; surface to 2,734 fathoms; between Canary and Azores Islands).

Beebe, 1929, p. 15. (1 specimen; ? mm.; ? fathoms; Hudson Gorge, northwest Atlantic).

Beebe, 1937, p. 205. (Preliminary list of 2,853 specimens; 9 to 22 mm.; 100 to 1,000 fathoms; Bermuda).

#### *M. (Myctophum) laternatum*:

Brauer, 1904, p. 388 (Key to species).

Brauer, 1906, p. 178, figs. 90-91. (63 specimens; ? to 22 mm.; ? fathoms; west coast Africa at Cape Verde, Sierra Leone, Gulf of Guinea, Indian Ocean, Sumatra, Bay of Bengal, Ceylon, Seychelles and Zanzibar, Gulf of Aden).

Zugmayer, 1911, p. 23. (1 specimen; 20 mm.; surface to 984 fathoms; Atlantic Ocean near Gibraltar).

Pappenheim, 1914, p. 193. (18 specimens; 11 to 19 mm.; 500 to 3,000 m. wire).

#### *M. laternatum atlanticum*:

Tåning, 1928, p. 56. (Key to new subspecies; 1 specimen; ? mm.; ? fathoms; Gibraltar).

Tåning, 1932, p. 118, figs. 1-2. (Description and synonymy).

LeGendre, 1934, p. 337. (Key to species).

Parr, 1934, p. 57. (Description).

#### *Diogenichthys laternatus*:

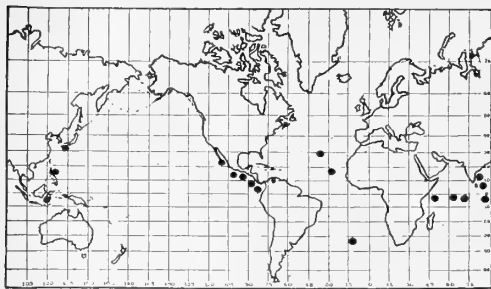
Bolin, 1939, pp. 92, 119, figs. 14, 15. (Key to species; detailed description; synonymy; 15 specimens; 11.9 to 25.1 mm.; lower California and Japan).

#### *Myctophum pterotum* (Alcock, 1890).

*Specimens taken by Eastern Pacific Expeditions*: 6 specimens; Eastern Pacific (*Zaca*) Expedition; surface to 500 fathoms; between 7° 08' and 16° 05' N. Lat., and 81° 57' and 98° 17' W. Long.; lengths 20 to 43 mm.; taken between Nov. 30, 1937 and March 20, 1938.

*Specimens previously recorded*: 180+ specimens; ? to 64 mm.; ? to 3,000 metres wire; mid- and south Atlantic and Indian Oceans, Borneo, Philippines, Japan, eastern

Pacific from tip of lower California to Panama.



TEXT-FIG. 8. Distribution of *Myctophum pterotum*.

**Photophore variation:** Both Bolin's and Parr's keys give 6-4 as the number of anal photophores of this species. Two of our six fish present exceptions to this combination, one of 38 mm. with 7-4, and another 43 mm. in length 6-4, 5-4.

**Luminous glands:** No luminous sex glands are visible on any of the specimens. Bolin (1939, p. 118) examined 28 specimens from the western Pacific measuring 30.8 to 53.1 mm. and states that "in most specimens, even the largest ones, no caudal luminous patches are developed."

**Vertical distribution:** Four specimens (34 to 43 mm.) taken at the surface after dark; two specimens (20 to 24 mm.) taken in a 500-fathom haul.

#### STUDY MATERIAL.

A total of 6 specimens was taken, as follows: Eastern Pacific (*Zaca*) Expedition, Station 193 L-1(3); 210 L-1(1); 225 T-1(2). For detailed trawling data, refer to *Zoologica*, Vol. XXIII, pp. 287-298.

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 116).

*Scopelus* (*Myctophum*) *pterotus*:

Alcock, 1890, p. 217. (60 specimens, including type; ? mm.; 98 to 102 fathoms; Bay of Bengal).

Alcock, 1896, p. 333. (Listing of previous reference).

*Myctophum pterotus*:

Goode & Bean, 1895, p. 5. (Reference to 60 specimens of Alcock's, listed above).

*Myctophum pterotum*:

Garman, 1899, p. 401. (Listing of Alcock's material).

Fowler, 1928, p. 70. (Description; synonymy).

Norman, 1929, pp. 512, 513, fig. 2. (Synonymy; reexamination of 8 specimens, including some of the types).

Parr, 1928, pp. 60, 67. (Key to species; synonymy; discussion of synonymy: *M. pterotum* vs. *M. fibulatum*).

Parr, 1929, p. 7. (Reexamination of type specimens; synonymy).

Parr, 1831, p. 22. (2 specimens; ? mm.; 525 to 1,800 fathoms; off west coast of Mexico).

Weber, 1913, pp. 86, 670. (5 specimens; 20 to 38 mm.; 6 fathoms; Macassar Straits near Borneo).

Weber & Beaufort, 1913, p. 157. (Description and synonymy).

*Myctophum gilberti*:

Evermann & Seale, 1907, p. 55, fig. 1. (4 specimens, including type; 54 to 64 mm.; ? fathoms; Philippines).

Gilbert, 1913, p. 81. (65 specimens; ? to 70 mm.; collected in market at Kagoshima, Japan).

*Myctophum* (*Myctophum*) *pterotum*:

Brauer, 1906, p. 182, figs. 93, 94. (6 specimens; ? to 61 mm.; 821 to 1,368 fathoms; Indian Ocean).

Barnard, 1925, p. 242. (Description).

Pappenheim, 1914, p. 193. (10 specimens; 13 to 18 mm.; ? to 3,000 metres wire; mid-north Atlantic).

*Myctophum pterotum panamense*:

Tåning, 1932, p. 129, fig. 3. (? specimens; 28 to 36 mm.; ? fathoms; Gulf of Panama).

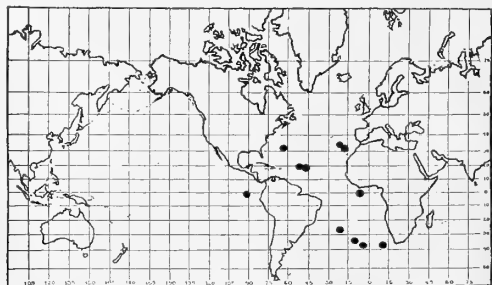
*Myctophum* (*Benthosema*) *pterotum*:

Bolin, 1939, pp. 92, 116, fig. 13. (Key to species; synonymy; description; 28 specimens; 30.8 to 53.1 mm.; ? fathoms; Japan, Philippines).

*Myctophum rarum* (Lütken, 1892).

**Specimens taken by the Eastern Pacific Expeditions:** 1 specimen; *Arcturus* Oceanographic Expedition; 500 fathoms; 0° 17' S. Lat., 91° 34' W. Long.; length 28 mm.; June 9, 1925.

**Specimens previously recorded:** 16 specimens; 21 to 40 mm.; ? to 1,640 fathoms; north and south Atlantic. Our specimen is the first to be recorded from the Pacific.



TEXT-FIG. 9. Distribution of *Myctophum rarum*.

**Photophore variation:** The single specimen corresponds in all details with the description of the species, having only two SAO and with a greater space between the first and second anterior anal photophores than between the others.

**Luminous glands:** This specimen, a male, has a very long and definite supracaudal gland, five plates running together with only faintly distinct divisions.

#### STUDY MATERIAL.

One specimen was taken, as follows: *Arcturus* Expedition, Station 84 Pt-3(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1928, p. 59).

*Scopelus (Rhinoscopelus) rarus*:

Lütken, 1892a, p. 246. (Key to species; description of type specimens; 4 specimens; 38 to 40 mm.; ? fathoms; north and south Atlantic).

?*Rhinoscopelus rarus*:

Goode & Bean, 1895, p. 91. (Description).

Jordan & Evermann, 1896, p. 569. (Description).

*Myctophum rarum* *forma integer*:

Brauer, 1904, p. 390. (Key to species; 1 specimen; 23 mm.; 1,640 fathoms; Gulf of Guinea).

Brauer, 1906, p. 204. (Further description).

Pappenheim, 1914, p. 197. (1 specimen; 31 mm.; 1,640 fathoms; south Atlantic).

LeGendre, 1934, p. 337. (Key to species).

?*Rhinoscopelus (Loweina) rarus*:

Fowler, 1925, No. 162, p. 2. (Listing only as new sub-genus "*Loweina*").

*Myctophum rarum*:

(Not Brauer 1906, pp. 163, 404; not Barnard 1925, p. 245).

Parr, 1928, p. 59. (Key to species and synonymy).

Tåning, 1928, p. 55. (Key to species).

Tåning, 1932, p. 155. (Description and figure).

LeGendre, 1934, p. 337. (Key to species).

Beebe, 1937, p. 205. (Preliminary list; 10 specimens; 21 to 26 mm.; 500 to 1,000 fathoms; Bermuda).

***Myctophum reinhardti* (Lütken, 1892).**

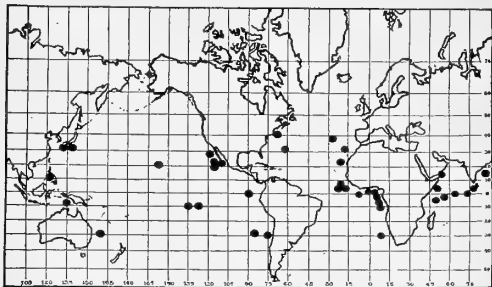
**Specimens taken by Eastern Pacific Expeditions:** 131 specimens; *Arcturus* Oceanographic Expedition; surface to 1,000 fathoms; between 2° S. and 2° 12' N. Lat., and 88° 11' and 91° 53' W. Long.; lengths 10 to 17 mm.; between April 14 and June 13, 1925.

24 specimens; Templeton Crocker Expedi-

tion; surface to 400 fathoms; between 18° 44' and 25° 25' N. Lat., and 108° 49' and 110° 33' W. Long.; lengths 13 to 51.5 mm.; between April 18 and May 7, 1936.

1 specimen; Eastern Pacific (*Zaca*) Expedition; surface; 28° 42' N. Lat., and 117° 50' W. Long.; length 51 mm.; Nov. 8, 1937.

**Specimens previously recorded:** 259 specimens; ? to 57 mm.; surface to 2,187 fathoms; north west Atlantic, Azores, west and east coasts of Africa, Indian Ocean, Japan, Australia, mid-Pacific and eastern Pacific from lower California south to mid-Chile.



TEXT-FIG. 10. Distribution of *Myctophum reinhardti*.

**Photophore variation:** Anal photophore counts were made on 121 fish, the others being two rubbed or otherwise damaged. Photophores are distinct on fish as small as 8 mm. in length. The count reveals two dominant, numerical nodes, 5-6 and 6-7, comprising 52 fish and 43 per cent., and 36 fish or 30 per cent. of the whole, respectively. Extremes in numbers are 5-6 and 6-9, with only two fish showing the bilateral numerical asymmetry of 6-6, 6-5 and 6-6, 7-5.

**Luminous glands and sex proportions:** All of the 131 specimens taken on the *Arcturus* Expedition are young. Of the Templeton Crocker Expedition catch of 24, only four showed developed, sexual, luminous glands; three males of 46, 51 and 51.5 mm. with supracaudal glands well developed, and one female of 40 mm. with two small, separate, infracaudal glands.

**Vertical distribution:** The vertical distribution of the 156 specimens is as follows: surface (58 fish), 300 fathoms (11 fish), 400 (28), 500 (35), 600 (4), 800 (9) and 1,000 fathoms (11 fish).

This proportion of surface captures of 58 fish or only 37 per cent. of the whole is unusual, and would seem to indicate that this species lives at greater depths than other myctophids.

**Sociability:** Schooling is indicated by the fact that 62 fish, or 40 per cent. of the total were taken in four nets, whereas the remaining 94 were distributed among 34 nets, of which a single fish occurred in each of 15 nets.

**Food:** Our only notes on food is the record of copepods in eight fish, amphipods in three, and euphausiids in three other fish.

#### STUDY MATERIAL.

A total of 156 specimens was taken, as follows: *Arcturus* Expedition, Station 41 T-1(7); 49 T-2(1); 50 T-5(6); 52 T-1(2); 57 T-1(17); 78 T-1(4); 84 T-2(1); 84 T-8(3); 84 T-10(3); 84 T-10(6); 84 T-14(3); 84 Pt-3(1); 84 T-19(1); 84 T-19(1); 84 T-20(1); 84 T-21(2); 86 T-2(20); 86 T-2(2); 86 T-4(6); 86 T-5(8); 86 T-7(1); 86 T-9(1); 86 T-10(1); 86 Pt-1(2); 86 T-11(3); 87 T-2(7); 87 T-3(12); 87 T-5(1). Templeton Crocker Expedition, Station 149 L-1(1); 158 T-2(1); 159 T-1(1); 159 T-2(2); 138 L-1(13); 160 L-1(1); 162 L-1(5). Eastern Pacific (*Zaca*) Expedition, Station 177 L-1(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 113).

##### *Scopelus reinhardtii*:

Lütken, 1892, p. 257, fig. 16. (*Partim*: 2 specimens, including type; ? to 43 mm.; ? fathoms, off Madeira and Liberia).

##### *Myctophum atratum*:

Garman, 1899, p. 268. (? specimens; ? mm.; 1,218 fathoms; southern part of Gulf of California).

##### *Myctophum braueri*:

Gilbert, 1905, p. 598. (Description; 17 specimens including type of 57 mm.; no other lengths given; surface; Hawaiian Islands).

##### *Myctophum lutkeni*:

Gilbert, 1905, pl. 70, fig. 1. (lapsus calami pro *Myctophum braueri*).

##### *Myctophum reinhardtii*:

Goode & Bean, 1895, p. 74. (Description). Waite, 1904, pp. 154, 194. (2 specimens; 35 and 45 mm.; ? fathoms; Australia).

Gilbert, 1908, p. 219. (6 specimens; young; ? fathoms; 300 miles east of Marquesas).

Gilbert, 1913, p. 80. (3 specimens; young; surface; off southwest coast of Japan).

Jordan & Jordan, 1925, p. 11. (References and synonymy).

Tåning, 1928, p. 57. (Key to species).

Parr, 1928, p. 66. (Key to species, synonymy).

Fowler, 1928, p. 70. (Synonymy).

Beebe, 1929, p. 16. (4 specimens; ? mm.; surface to 800 fathoms; Hudson Gorge, northwest Atlantic).

Beebe, 1937, p. 205. (Preliminary list; 72 specimens; 11 to 35 mm.; 100 to 1,000 fathoms; Bermuda).

##### *Myctophum benoiti reinhardtii*:

Brauer, 1904, p. 388. (Key to species).

Brauer, 1906, p. 185. (100 specimens; ? to 25 mm.; 670 to 2,187 fathoms; Gulf of Guinea, southwest Africa, Bay of Bengal, Seychelles Islands, Gulf of Aden, Ceylon, Indian Ocean, west coast of Chile).

Weber, 1913, p. 86. (5 specimens; 9 to 16 mm.; surface to 825 fathoms; Banda Sea, Almahera Sea, East Indies).

Weber & Beaufort, 1913, pp. 152, 155. (Key to species; synonymy and description).

Pappenheim, 1914, p. 193. (16 specimens; 15 to 32 mm.; ? to 1,642 fathoms; south Atlantic).

Barnard, 1925, p. 242. (References and brief description).

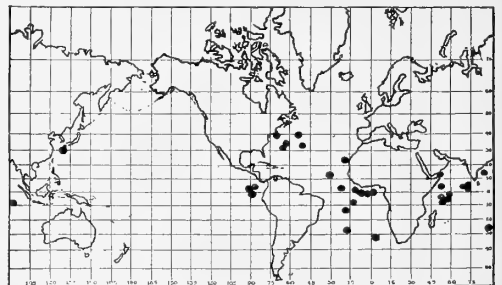
##### *Myctophum (Hygophum) reinhardtii*:

Bolin, 1939, pp. 93, 113-116, fig. 12. (Key; synonymy; description; 31 specimens, of which 7 were paratypes of *M. braueri*, Gilbert; 17.7 to 31.2 mm.; ? fathoms; Hawaiian Islands and Philippines).

##### *Myctophum valdiviae* Brauer, 1904.

*Specimens taken by Eastern Pacific Expeditions*: 35 specimens; *Arcturus* Oceanographic Expedition; 300 to 700 fathoms; between 6° 27' N. Lat., and 0° 17' S. Lat., and 91° 53' and 84° 35' W. Long.; lengths 8 to 23 mm.; between May 1 and June 13, 1925.

*Specimens previously recorded*: 924 specimens; ? to 23 mm.; surface to 2,260 fathoms; north and south Atlantic Ocean, west and east coasts of Africa, Indian Ocean, Japan and eastern Pacific off Cocos and Galápagos Islands.



TEXT-FIG. 11. Distribution of *Myctophum valdiviae*.

**Photophore variation:** All 35 specimens were in rather bad condition, with nearly all the anal photophores rubbed or torn away. The species is easily identified without them, it being the only *Myctophum* which has the four upper photophores above the lateral line. Because of the generally poor condition of the anal photophores,

nothing of interest could be determined in regard to their variation.

**Luminous glands:** The 35 fish measured from 8 to 23 mm. Of these 20 showed no signs of supracaudal luminous glands, and (with the exception of one fish of 16 mm.) were all 12 mm. or under in length. The distinction between male and female glands is not satisfactory enough to class the remaining 16 fish as anything but nearly or not quite adult.

**Breeding:** Fish No. 5569, a female of 22 mm., was taken 100 miles south of Cocos Island, on May 1. The ovaries were 3.5 mm. in length and the diameter of the eggs .28 mm. The total number of eggs about to be laid was 120.

**Vertical distribution:** All 35 fish were taken at depths from 300 to 700 fathoms; none at the surface. The relative numbers were 300 fathoms (4 fish); 400 (11); 500 (14); 600 (5); and 700 fathoms (1 fish).

**Sociability:** With only 35 specimens at hand it is difficult to hazard any opinion as to schooling, especially as 8 fish were taken in one net, and 8 others each in a single net.

**Food:** Copepods and amphipods were found in several stomachs.

#### STUDY MATERIAL.

A total of 35 specimens was taken, as follows: *Arcturus* Expedition, Station 59 T-4(1); 59 T-5(2); 59 T-9(1); 59 Pt-2(3); 61 T-3(3); 68 T-3(2); 74 T-8(1); 74 T-71(2); 74 T-74(2); 74 T-78(1); 84 T-1(1); 84 T-8(1); 84 T-20(1); 86 T-2(5); 86 T-8(1); 87 T-2(8). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

#### REFERENCES AND SYNONYMY.

(References accepted according to Parr, 1928, p. 57).

##### *Myctophum valdiviae*:

Brauer, 1904, p. 398, fig. 6. (Preliminary listing of 68 specimens, including type; details in following reference).

Brauer, 1906, p. 206, fig. 127. (68 specimens; 8 to 23 mm.; 274 to 2,260 fathoms; Atlantic Ocean, south of Canary Islands, Gulf of Guinea, 500 miles west of southwest Africa, Indian Ocean, between Aden and Madagascar, mid-ocean between Ceylon and Zanzibar, Cocos Island, Bay of Bengal).

Gilbert, 1913, p. 84. (1 badly injured specimen; ? mm.; ? to 300 fathoms; Japan).

Tåning, 1918, p. 151, fig. 47. (Description of post-larvae; 4 specimens; 1 adult and 3 post-larvae; 4.7 to 15 mm.; ? fathoms; mid-ocean northwest and southwest of Bermuda).

Tåning, 1928, p. 57. (Key to species).

Tåning, 1932, p. 121, figs. 1, 2. (Description).

Parr, 1928, p. 57. (Key to species; synonymy).

LeGendre, 1934, p. 335. (Key to species).  
Beebe, 1929, p. 15. (4 specimens; ? mm.; ? fathoms; Hudson Gorge, northwest Atlantic Ocean).

Beebe, 1937, p. 205. (Preliminary list; 846 specimens; 9 to 23 mm.; 300 to 1,000 fathoms; Bermuda).

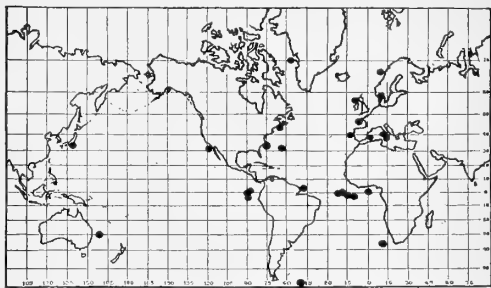
##### *Myctophum (Myctophum) valdiviae*:

Pappenheim, 1914, p. 194. (16 specimens; 9 to 24 mm.; 800 to 3,000 metres; north and south Atlantic).

##### *Lampanyctus elongatus* (Costa, 1844).

**Specimens taken by Eastern Pacific Expeditions:** 3 specimens; *Arcturus* Oceanographic Expedition; surface to 700 fathoms; between 2° 00' S. Lat. and 4° 50' N. Lat., and between 87° 00' and 89° 48' W. Long., lengths, 25, 72.5 and 83 mm.; taken April 3 and 23, May 31, 1925.

**Specimens previously recorded:** 706 specimens; ? to 153 mm.; surface to 2,600 fathoms; western Atlantic from Greenland south to Cape Horn, eastern Atlantic from mid-Norway and Mediterranean south to Cape of Good Hope, Australia, Japan, eastern Pacific from San Diego to Galápagos. Our specimens extend the range to the Galápagos and Cocos Islands. A widely distributed but rare species.



TEXT-FIG. 12. Distribution of *Lampanyctus elongatus*.

**General data:** Our three specimens show the following details: Cat. No. 5214a, sex uncertain, 25 mm. in length, anal photophores 9-6, 9-5. Cat. No. 5429, a female, 83 mm., anal photophores 8-?, 8-?, taken April 23, 1925, ovaries injured but many eggs visible; not countable but almost ready to be deposited. Cat. No. 6053, female, 72.5 mm.; anal photophores 8-6, 9-6. Two small, infracaudal luminous glands just appearing. Eggs undeveloped. Anal photophore counts of other authors are 7-9, 6-7; 7-9, 5-7; and 9-6, 6-7.

**General color:** Cornea over pupil reflecting iridescent green in all illuminations; iris dark brown except for the inferoposterior third which is brilliant coppery gilt; body in general brownish-black; glints of blue and green on opercles and body, but

scales are colorless. All large, round photophores are pink, smaller ventral ones silvery. All light given off is decidedly pink.

*Food:* The 83 mm. female had eaten two amphipods and one euphausiid.

#### STUDY MATERIAL.

A total of 3 specimens was taken, as follows: *Arcturus* Expedition, Station 33 Pt-1 (1); 52 T-1 (1); 74 T-35 (1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 151).

##### *Scopelus elongatus:*

Costa, 1844, p. 2, pl. 38. (Original description; reference not seen; Naples, fide; Jordan & Evermann, 1896).

Canestrini, 1870, p. ? (Reference not seen).

Steindachner, 1881, p. 397. (Description and discussion of synonymy of ? specimens in Vienna Museum; 135 to 150 mm.; ? depth, ? locality).

Vinciguerra, 1885, p. 462. (Description and synonymy).

Raffaele, 1889, p. 184, fig. 11. (Discussion of synonymy).

Lilljeborg, (1884-91), p. ? (Reference not seen).

Lütken, 1892a, p. 264. (Description and key to species; 4 specimens; about 80 to 84 mm.; ? fathoms; Greenland, Gulf of Guinea and south of Cape of Good Hope).

Koehler, 1896, p. 506. (1 specimen; 62 mm.; 760 fathoms; off Lorient, France).

Holt & Byrne, 1905, p. 23. (1 specimen; ? mm.; 350 fathoms; northeast coast of Ireland).

Holt & Byrne, 1911, p. 24, fig. 7. (Description and synonymy).

##### *Scopelus crocodilus:*

Cuvier & Valenciennes, 1849, vol. 20, p. 332. (Reference).

Cuvier & Valenciennes, 1849, vol. 22, p. 447. (Description).

##### *Scopelus pseudocrocodilus:*

Moreau, 1891, p. 84, fig. 227. (Description).

Brauer, 1906, p. 233. (Synonymized with *M. (Lampanyctus) elongatum*).

##### *Scopelus kroyeri:*

Malm, 1863, p. 100. (Reference not seen).

Brauer, 1906, p. 232, figs. 152, 153. (Synonymizes this with *M. (Lampanyctus) elongatum*).

Winther, 1879-80, p. 42. (Brief reference).

Collet, 1880, p. 162. (1 specimen, found in stomach of *gadus morrha*).

##### *Scopelus resplendens:*

Günther, 1864, vol. 22, p. 415. (Description and synonymy).

##### *Scopelus (Notoscopelus) elongatus:*

Günther, 1864, vol. 22, p. 415. (Description and synonymy).

##### *Notoscopellus brachychir:* (error in type).

Eigenmann & Eigenmann, 1889, p. 126. (3 specimens; ? mm.; 45 fathoms; Cortez Bay, San Diego).

##### *Notoscopelus brachychir:*

Eigenmann & Eigenmann, 1890, p. 23. (Reference).

##### *Notoscopelus resplendens:*

Goode & Bean, 1895, p. 83, fig. 94. (Description and key).

##### *Notoscopelus elongatus:*

Goode & Bean, 1895, p. 83. (Description and key).

Bolin, 1939, pp. 93, 151, 152, fig. 29. (Key; synonymy and description; 2 specimens; 110 and 113.5 mm.; ? fathoms; Misaki Sea, Japan).

##### *Notoscopelus quercinus:*

Goode & Bean, 1895, p. 83, fig. 97. (3 specimens; ? to 125 mm.; ? to 781 fathoms; north Atlantic, off Cape Cod, Massachusetts, and coast of Virginia).

##### *Notoscopelus ejectus:*

Waite, 1904, p. 150, pl. 18, fig. 2. (1 specimen; 40.5 mm.; ? fathoms; Australia).

##### *Catoblemmella brachychir:*

Eigenmann & Eigenmann, 1890, p. 23. (Reference).

##### *Scopelus (Lampanyctus) elongatus:*

Lütken, 1892, p. 233. (Reference to specimens described under *Scopelus elongatus*).

Carus, 1889-1893, p. 565. (Description).

##### *Macrostoma angustidens:*

Jordan & Evermann, 1896, p. 555. (Description).

##### *Macrostoma quercinum:*

Jordan & Evermann, 1896, p. 554. (Description).

##### *Macrostoma brachychir:*

Jordan & Evermann, 1898, p. 2826. (Name listed).

##### *Macrostoma quercinum japonicum:*

Tanaka, 1908, p. 5, pl. 1, fig. 3. (Description).

##### *Macrostoma japonicum:*

Tanaka, 1911, p. 59, pl. 15, fig. 51. (Redescription of type specimen reported in previous reference).

*Myctophum elongatum*:

Collet, 1884, p. 104. (Description; discussion of synonymy; 5 specimens; 128 to 145 mm.; ? fathoms; coast of Norway, Trondheim and vicinity).

Smitt, 1895, p. 937, fig. 234. (Detailed description).

Sanzo, 1918a, p. 4. (Description of young).

*Myctophum (Lampanyctus) elongatum*:

Brauer, 1906, p. 232, figs. 152, 153. (Key; description; synonymy; 7 specimens; 15 to 125 mm.; 380 to 2,187 fathoms; Gulf of Guinea, west of Cape Colony).

Fage, 1910, p. 15, fig. 13. (Description).

Zugmayer, 1911, p. 37. (1 specimen; 57 mm.; 2,600 fathoms; off west coast of Portugal).

Pappenheim, 1914, p. 196. (6 specimens; 22 to 29 mm.; ? to 1,642 fathoms; south Atlantic).

Alaejos, 1919, p. ? (Reference not seen).

Barnard, 1925, vol. 21, p. 238. (Description).

*Myctophum (Lampanyctus) quercinum*:

Brauer, 1906, p. 166. (Key to species).

*Lampanyctus japonicus*:

Gilbert, 1913, p. 99. (Brief discussion).

*Lampanyctus resplendens*:

Richardson, 1844, p. 42, pl. 27, figs. 16-18. (1 specimen; 112 mm.; ? fathoms; ? locality).

Matsubara, 1938, p. 53, fig. 10. (Description; 3 specimens; 123 to 153 mm.; about 150 fathoms; Japan).

*Lampanyctus elongatus*:

Gilbert, 1913, p. 99. (Reference; discussion of *L. japonicus*).

Tåning, 1918, pp. 103-106, figs. 40, 41. (Detailed description of both young and adults; distribution map; propagation etc.; 651 specimens; ? to 60 mm. surface to 670 fathoms; western Mediterranean and Atlantic Ocean).

Tåning, 1928, p. 64. (Key to species).

Tåning, 1932, p. 124, figs. 1, 2. (Description).

Parr, 1928, p. 80. (Key to species; synonymy).

Parr, 1929, p. 14. (Additional synonymy).

Norman, 1930, p. 329. (4 specimens; 30 to 53 mm.; surface to 547 fathoms; mid and south Atlantic).

LeGendre, 1934, p. 343. (Key to species).

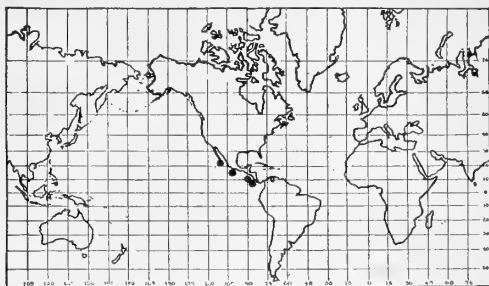
Beebe, 1937, p. 204. (Preliminary list; 11 specimens; 13 to 30 mm.; 400 to 1,000 fathoms; Bermuda).

*Lampanyctus idostigma* Parr, 1931.

*Specimens taken by Eastern Pacific Expeditions*: 12 specimens; Eastern Pacific

(Zaca) Expedition; 300 to 500 fathoms; between 8° 03' and 9° 12' N. Lat., and 83° 12' and 85° 10' W. Long.; lengths 16 to 37 mm.; between Feb. 7 and March 10, 1938.

*Specimens previously recorded*: 27 specimens; 50 to 76 mm.; 100 to 200 fathoms; Eastern Pacific from tip of Lower California to Nicaragua. Our collection extends the range to southern Costa Rica.



TEXT-FIG. 13. Distribution of *Lampanyctus idostigma*

*Anal photophores*: Our 12 specimens, ranging from 16 to 37 mm.; are all too immature to be sexed. The photophore arrangement is as follows: (5 specimens) 6-6; (4) 5-6; (2) 5-6, 6-6; and (1 specimen) 6-6, 6-7.

*General data*: Three fish were taken at 300 fathoms and nine at 500 fathoms. There is no hint of schooling as the 12 fish were scattered among eight nets. All the evidence points to this species living in deep water. Our fish were all taken at two localities off Costa Rica, 150 miles apart.

## STUDY MATERIAL.

A total of 12 specimens was taken, as follows: Eastern Pacific (Zaca) Expedition, Station 210 T-1 (2); 210 T-3 (1); 210 T-6 (1); 210 T-7 (1); 210 T-8 (3); 210 T-10 (1); 219 T-1 (1); 219 T-2 (2). For detailed trawling data, refer to *Zoologica*, Vol. XXIII, pp. 287-298.

## REFERENCES AND SYNONYMY.

*Lampanyctus idostigma*:

Parr, 1931, p. 32, fig. 13. (27 specimens, including type; 50 to 76 mm.; 300 to 625 fathoms cable; Pacific coast of Nicaragua, off southern Mexico, Gulf of California).

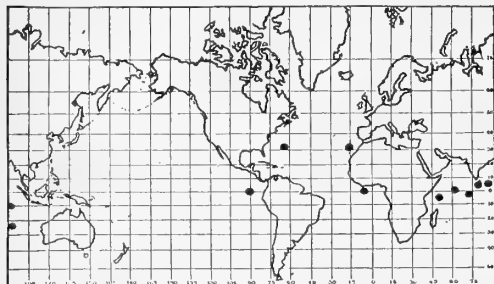
Bolin, 1939, pp. 93, 138, fig. 22. (Key to species; redescription of 2 of Parr's specimens).

*Lampanyctus longipes* (Brauer, 1906).

*Specimens taken by Eastern Pacific Expeditions*: 1 specimen; *Arcturus* Oceanographic Expedition; 500 fathoms; at 0° 40' N. Lat., and 91° 47' W. Long., length 21 mm.; taken June 12, 1925.



*Specimens previously recorded:* 18 specimens; surface to 1,230 fathoms; 11 to 32 mm.; rare but widely distributed. Bermuda, west coast of Africa, Indian Ocean, Bay of Bengal. Our record is the first for the Pacific, and was off the Galápagos.



TEXT-FIG. 14. Distribution of *Lampanyctus longipes*.

Our fish, 21 mm., was too young for sexing; its anal photophore count was 5-3, 5-3.

#### STUDY MATERIAL.

One specimen was taken, as follows: *Arcturus* Expedition, Station 86 T-2(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1928, p. 82).

#### *M. (Lampanyctus) longipes:*

Brauer, 1906, p. 236, fig. 155. (Original description; 14 specimens, including types; 11 to 32 mm.; surface to 1,230 fathoms; Madeira, Gulf of Guinea, Seychelles Islands, Bay of Bengal, south of Ceylon, Indian Ocean).

#### *Lampanyctus pyrsobolus longipes:*

Tåning, 1928, p. 65. (Key to species).

LeGendre, 1934, p. 344. (Key to species).

#### *Lampanyctus longipes:*

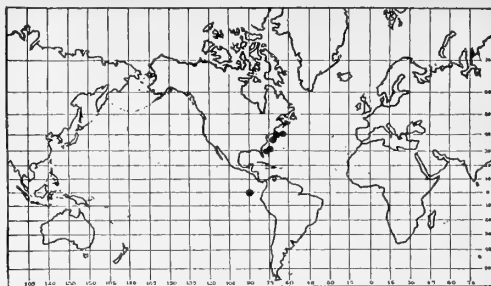
Parr, 1928, p. 82. (Key to species; synonymy).

Beebe, 1937, p. 204. (Preliminary list; 4 specimens; 12 to 20 mm.; 800 to 1,000 fathoms; Bermuda).

#### *Lampanyctus macdonaldi* (Goode & Bean, 1895).

*Specimens taken by Eastern Pacific Expeditions:* 3 specimens; *Arcturus* Oceanographic Expedition; 400 fathoms; between 0° 00' equator and 91° 53' W. Long.; lengths 20 to 29 mm.; June 13, 1925.

*Specimens previously recorded:* ? specimens; lengths ? to 154 mm.; ? to 1,467 fathoms; northwestern Atlantic. Our specimens are the first recorded from the Pacific Ocean.



TEXT-FIG. 15. Distribution of *Lampanyctus macdonaldi*.

*Photophore variation:* Our three specimens, (Cat. No. 6365a), taken 21 miles north of Narborough, Galápagos, show the following anal photophore count: 1 specimen 20 mm. 6-6-4 on both sides; 1 specimen 27 mm. 6-6-4 and 6-7-4; 1 specimen 29 mm. 6-6-4 on both sides.

#### STUDY MATERIAL.

A total of 3 specimens was taken, as follows: *Arcturus* Expedition, Station 87 T-2 (3). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1929, p. 20).

#### *Nannobranchium macdonaldi:*

Goode & Bean, 1895, p. 94, fig. 110, pl. 29. (Original description; ? specimens, including type; ? to 154 mm.; ? to 1,467 fathoms; northwestern Atlantic).

Jordan & Evermann, 1896, vol. 1, p. 563. (Description).

Tåning, 1928, p. 69. (Reference to synonymy).

#### *Lampanyctus macdonaldi:*

Parr, 1929, p. 20, fig. 9. (Redescription of type specimen and synonymy).

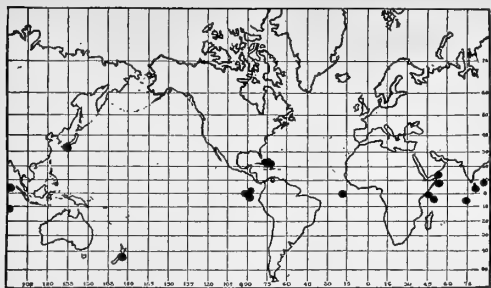
#### *Lampanyctus macropterus* (Brauer, 1904).

*Specimens taken by Eastern Pacific Expeditions:* 150 specimens; *Arcturus* Oceanographic Expedition; surface to 1,000 fathoms; between 2° 00' S. and 4° 50' N. Lat., and 87° 00' and 91° 53' W. Long.; lengths 16 to 70 mm.; taken between April 22 and June 13, 1925.

*Specimens previously recorded:* 29 specimens; ? to 105 mm.; surface to 1,642 fathoms; West Indies, south Atlantic, north Indian Ocean, Bay of Bengal, Japan. Our specimens, all from the Galápagos, are the first recorded from the eastern Pacific.

*Photophore variation:* Photophore count of 137 fish shows them in general to be symmetrical, 30 per cent. or 42 specimens hav-





TEXT-FIG. 16. Distribution of *Lampanyctus macropterus*.

ing 5-9 anal photophores; 27 per cent. or 37 specimens having 5-8 anal photophores, and the balance are divided into the following combinations: 4-8, 4-10, 4-11, 5-7, 5-10, 5-11, 6-8, 6-9, and the asymmetrical combinations of 5-7, 4-8; 5-8, 5-7; and 5-9, 5-7.

**Development:** All of the 150 specimens were measured with this result: 84 fish or 56 per cent. were 16 to 36 mm. and 66 fish or 44 per cent. from 37 to 70 mm. in length.

**Eggs:** Three females (Cat. No. 6057), measuring 53, 55 and 59 mm. had eggs present, while another female, measuring 50 mm. (same Cat. No.) was without developed eggs. These were taken at Station 74, T-41, 42, 60 miles south of Cocos Island on June 1, 1925.

**Vertical distribution:** Of the entire catch, 46 fish or 33 per cent. were taken at the surface. Of the remainder, 70 per cent. were brought up from 400 and 500 fathoms. An unusual fact is that 11 of the 46 surface fish were taken in full sunlight, in a haul made from 9.30 to 11.00 A.M. These 11 were all young (18 to 24 mm.), while the remaining surface fish taken after dark were much larger (35 to 58 mm.) more nearly adult.

**Sociability:** Schooling is definitely indicated. Seventy-five fish or 50 per cent. were taken in five nets, an average of 15 fish to a net, while the rest were distributed among 24 nets, averaging two and a half fish to each.

**Food and Anatomy:** On May 24, 1925, sixty miles south of Cocos Island, at 8.00 to 8.30 P.M. from a rainy and a rough sea, I drew a surface net containing among other fish 13 *Lampanyctus macropterus*. These were large (50 to 70 mm.) and very vigorous and active. A male of 65 mm. appeared to have gorged itself, and I dissected it for food. The swim bladder was fully inflated, silvery white and 20 mm. long. The anterior end was rounded and 5.5 mm. in diameter. This thickness was sustained posteriorly for 12 mm. when the organ tapered rapidly for the posterior 8 mm. to end in a

fine point. The lining of the body cavity was slightly pigmented, while the stomach, unlike any of the other organs, was jet black.

The fish had already fed well although it was so early in the evening. The contents comprised 9 fish eggs, 1 mollusk egg-mass, 1 small sagitta, 5 young euphausiids, 3 hyperid amphipods, 6 small calanids, and 1 *Eucalanus elongatus*.

**Luminescence and viability:** The following notes are from my Journal made on May 25, 1925, upon fish from a surface haul made sixty miles south of Cocos Island, in the darkroom of the *Arcturus*. There were a number of *Noctiluca* and *Sapphirina* in the water but we had little trouble in differentiating between their light and that of the myctophids. We tested the fish in artificial sea water but if anything their light was exhausted sooner than in the warmer, normal salt water. There was no reaction to three drops of ammonia, nor to a slight shock of electricity sent through the water. When sent through the fish they died immediately.

One observation made again and again during the evening was of an obliterative flashing, repeated so identically that there could be no question as to its repeated occurrence, whatever may be the precise interpretation. The fish was lighted up dully and in the indirect manner for which as yet I have no explanation. It swam slowly about and when it encountered another fish or my finger, it turned with a quick flick of the tail, emitting a very brilliant flash from its two precaudal photophores, and then vanished completely. This quenching was achieved in one of two diverse ways. If the fish was swimming upside down, as it often does, it turned over after the caudal flash and exposed the unlighted dorsal area, or it sometimes actually turned out every light, from head to tail.

The actions of various individuals differed widely. One which was brought in some time after our first specimens had begun to die down, swam continually on its back and glowed dully from every photophore. Rarely it blackened, and twice I saw sets of four and of six photophores respectively, lit as individual units. The brightest light on the entire body was the most dorsal of the pre-pectoral set.

When first caught, even when dipped gently in a net from the companionway and dropped at once into a bucket of water, the immediate instinct of the fish is to descend. It swims in small circles, making constant nose dives and bumping its head against the bottom.

Two other *Lampanyctus* lighted up as a whole, but the general effect was always of separate lights, the photophores not being

so near together as in *M. coccoi* and the silver scales being absent. It is curious that although *coccoi* is so intensely active, its scales are far less deciduous than those of other species. Holding *L. macropterus* by the head resulted in intense general illumination, and even in the air the light lasted a considerable time before being doused. When it went out, the head and tail lights were sustained alone. When a male was held by the head, while the entire under surface was aglow, the dorsal aspect was entirely black except for the median, dorsal, caudal plates.

A few days later several large specimens of this species were watched. In the dark-room they glowed dully, never as brilliantly in general as *M. coccoi*. Their lunate light organs seemed to diminish the glow. They swam upside down, and suddenly one made a rush, seized the other by the jaw and began pushing him about. Both seemed to have the same grip, and the pushing on the part of both kept up until death. The whole affair was of course accidental. Sometime after apparent death, the jaw lights glowed faintly. During life these six lights were the dominant ones, with the exception of the succeeding pair on the isthmus, which occasionally shone with a very powerful glare. When the entire fish was aglow, a hand lens showed every ventral light shining full strength, but to the unaided eye the illumination was indefinite, indirect. In daylight the photophores are bright purple.

#### STUDY MATERIAL.

A total of 150 specimens was taken, as follows: *Arcturus* Expedition, Station 50 T-5(2); 74 T-1(24); 74 Pt-1(3); 74 Pt-2(1); 74 T-7(1); 74 T-10(4); 74 T-11(3); 74 T-15(2); 74 T-16(1); 74 T-21(1); 74 T-22(14); 74 Ot-2(1); 74 Ot-3(1); 74 T-27(1); 74 T-35(1); 74 T-35(1); 74 T-41(3); 74 T-43(7); 84 T-2(24); 84 T-10(1); 84 T-10(2); 84 T-10(5); 84 T-14(10); 84 Pt-3(2); 84 Pt-3(14); 86 T-2(2); 86 T-2(1); 86 T-4(2); 86 T-5(3); 86 T-11(3); 87 T-2(6); 87 T-6(4). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1931, p. 28).

*Myctophum* (*Lampanyctus*) *macropterus*:

Brauer, 1904, pp. 381, 404, fig. 5. (Key and description of type specimen).

Brauer, 1906, p. 249, figs. 166, 167. (22 specimens; ? to 65 mm.; 547 to 1,368 fathoms; Indian Ocean, Bay of Bengal, Ceylon, Cocos, Seychelles Islands, Gulf of Aden, North Africa, (*partim*) and fig. 166, nec. fig. 167).

Pappenheim, 1914, p. 196. (1 specimen; 63 mm.; ? to 1,642 fathoms; south Atlantic).

*Lampanyctus macropterus*:

Gilbert, 1913, p. 106. (1 specimen; 105 mm.; 703 (?) fathoms; Kagoshima, Japan).

Regan, 1916, p. 140. (1 specimen; 10 mm.; 2 fathoms; New Zealand).

Parr, 1928, pp. 88, 110, fig. 20. (Key to species; synonymy; description; 4 specimens; ? mm.; 7-8,000 feet wire; West Indies).

Parr, 1931, pp. 25, 28, fig. 10. (nec. Parr, 1928, p. 110; key to species; discussion; synonymy).

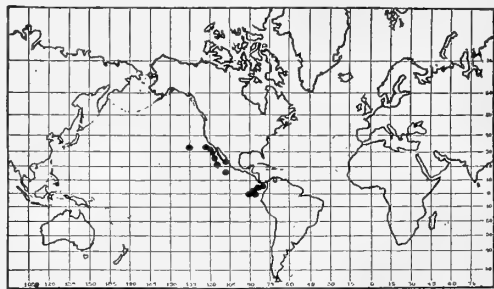
*Lampanyctus mexicanus* (Gilbert, 1890).

*Specimens taken by Eastern Pacific Expeditions*: 36 specimens; *Arcturus* Oceanographic Expedition; 255 to 833 fathoms; between 0° 17' S. and 6° 24' N. Lat., and between 81° 18' and 91° 34' W. Long.; lengths 13.5 to 64 mm.; March 30 to June 9, 1925.

177 specimens: Templeton Crocker Expedition; surface to 500 fathoms; between 23° 25' and 30° 00' N. Lat., and 108° 31' and 116° 27' W. Long.; lengths 19 to 63 mm.; March 28 to May 23, 1936.

4 specimens; Eastern Pacific (*Zaca*) Expedition; 500 fathoms; between 5° 10' and 9° 12' N. Lat., and 78° 42' and 85° 08' 30" W. Long.; lengths 18 to 52 mm.; February 7 to March 26, 1938.

*Specimens previously recorded*: 143+ specimens; ? to 64.7 mm.; surface to 1,218 fathoms; eastern Pacific, from California at Point Conception south to Ecuador.



TEXT-FIG. 17. Distribution of *Lampanyctus mexicanus*.

*Photophore variation*: Ten of the 36 fish from the *Arcturus* had asymmetrical counts; 15 were symmetrical, 5-9; and the remaining 11 were about equally divided among the symmetrical combinations of 4-8, 4-9, 4-10, 5-8, 5-10.

The count on 25 fish from the Templeton Crocker group showed that 13 specimens, or 50 per cent., had the 4-9 pattern, with the others varying from 4-8 to 5-9. Three individuals have asymmetrical patterns on the two sides of the body.

*Vertical distribution*: *Lampanyctus mexicanus* is a deep water species as the vertical distribution of our catch well shows. 106

fish (59 per cent.) were taken at 300 fathoms; 53 (30 per cent.) at 400; and 21 fish (11 per cent.) from 500 fathoms. Only a single individual was captured in a surface haul.

**Sociability:** Schooling was more evident than in any other species encountered. About 60 per cent. of the entire catch, or 105 fish, was taken in a single net, but this is only part of the truth. The same school evidently extended throughout 200 vertical fathoms, for on April 17, three nets on the same wire, drawn from 3.45 to 5.00 P.M., at 300, 400 and 500 fathoms contained 105, 25 and 19 fish respectively, or four-fifths of all of this species taken on all three expeditions. The remaining fish were distributed as follows: one net (13 fish), one net (10 fish), and nine nets (1 fish each).

#### STUDY MATERIAL.

A total of 217 specimens was taken, as follows: *Arcturus* Expedition, Station 26 Pt-1(1); 39 T-4(1); 59 Pt-2(1); 66 Pt-1(1); 74 Pt-1(1); 74 Pt-3(3); 74 Ot-3(1); 74 Ot-4(1); 84 T-2(5); 84 Pt-1(7); 84 T-8(4); 84 T-14(8); 84 Pt-3(2). Templeton Crocker Expedition, Station 130 T-1(13); 139 T-2 and T-3 and T-4(10); 148 T-2(105); 148 T-3(25); 148 T-4(19); 148 T-8(1); 158 T-3(1); 158 T-4(1); 159 T-1(1); 174 L-1(1). Eastern Pacific (*Zaca*) Expedition, Station 210 T-6(1); 210 T-10(1); 227 T-1(1); 230 T-1(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 135).

##### *Myctophum mexicanum*:

Gilbert, 1890, p. 51. (6 specimens, including type; ? to 50 mm.; 306 to 857 fathoms; Gulf of California).

##### *Scopelus mexicanus*:

Lütken, 1892, p. 266. (Name listed).

##### *Nannobrachium mexicanum*:

Goode & Bean, 1895, p. 512. (Name listed).

##### *Myctophum ocaleum*:

Garman, 1899, p. 260, pl. 56, fig. 2. (? specimens; ? mm.; surface to 1,218 fathoms; off Pacific coast lower California, south to Ecuador).

##### *Myctophum (Lampanyctus) mexicanum*:

Brauer, 1904, p. 396. (Key to species).

##### *Myctophum (Lampanyctus) ocaleum*:

Brauer, 1906, p. 167. (Key to species).

##### *Lampanyctus ocaleus*:

Parr, 1928, p. 85. (Key and synonymy).

Parr, 1934, p. 46. (Synonymizes with *L. mexicanus*).

##### *Lampanyctus mexicanus*:

Parr, 1928, p. 84. (Key and synonymy).

Parr, 1929, p. 15, fig. 6. (Key and further description of type).

Parr, 1931, p. 30, fig. 12. (23 specimens; ? to 60 mm.; ? to 286 fathoms; eastern Pacific coast of Mexico).

Bolin, 1939, pp. 93, 135, fig. 21. (Key; synonymy; description; 114 specimens; 15.5 to 64.7 mm.; ? fathoms; from Point Conception, California south to Gulf of California. These include 2 co-types and 4 of Garman's *M. ocaleum*).

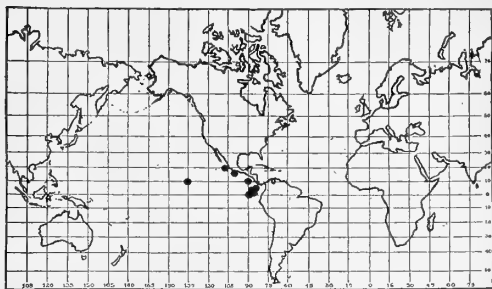
##### *Lampanyctus omostigma* Gilbert, 1908.

**Specimens taken by Eastern Pacific Expeditions:** 246 specimens; *Arcturus* Oceanographic Expedition: surface to 1,200 fathoms; between 2° 00' S. and 6° 27' N. Lat., and 83° 33' and 91° 53' W. Long.; lengths 12 to 68 mm.; between April 22 and June 13, 1925.

94 specimens; Eastern Pacific (*Zaca*) Expedition: 300 to 500 fathoms; between 5° 10' and 17° 45' N. Lat., and 78° 42' 71" and 103° 05' W. Long.; lengths 13 to 96 mm.; between Nov. 23, 1937 and March 26, 1938.

**Specimens previously recorded:** 30 specimens; ? to 62 to ? mm.; surface to 200 fathoms; mid-Pacific near Marquesas Islands and eastern Pacific from Mexico to Galápagos. Our collection establishes the species as occurring nearly 800 miles south of the earlier known range.

After careful examination of our specimens we fail to find sufficient consistent variation to differentiate these eastern Pacific fish as *Lampanyctus omostigma parvicauda* (Parr, 1931, p. 26, fig. 9).



TEXT-FIG. 18. Distribution of *Lampanyctus omostigma*.

**Photophore variation:** The range in number of anal photophores is 4-8 and 6-10, with the dominant nodes at 5-8 and 5-9, appearing on 34 specimens each, totaling 68 specimens or more than 41 per cent. of the 163 specimens examined. Forty-four specimens or 27 per cent. were asymmetrical in the bilateral count.

**Breeding:** One female (Cat. No. 6057) 59 mm. in length was in full breeding condition. This fish was taken at the surface on June 1; the ovaries were 13 mm. in length, and the total number of enlarged eggs about 2,700.

**Vertical distribution:** This is one of the deeper-living species of the family. About one-third of the entire catch came from a depth of 500 fathoms, with numbers grading sharply down above and below this depth. The data is as follows: surface (96 fish), 100 fathoms (4 fish), 300 fathoms (18 fish), 400 fathoms (12 fish), 500 fathoms (130 fish), 600 fathoms (62 fish), 700 fathoms (11 fish), 800 fathoms and deeper (7 fish).

**Sociability:** The only real hint of schooling is in one surface net which captured 90 fish within an hour, 8.30 to 9.30 P. M. Of the remaining 54 nets, 28 contained only one or two fish each, while six nets took numbers ranging from 10 to 28 individuals.

**Luminescence and viability:** Three large fish were taken into the darkroom as soon as caught. They showed at first no general luminescence but a multitude of bright sparks. These increased upon agitation of the water and seemed to come from every photophore on the body. Only twice thereafter, within a space of five minutes, did I see very briefly the dull, indirect glow so characteristic of a species such as *Myctophum affine*. The light was clear white and brightly illuminated the entire dish and all the surrounding plankton. Usually the fish lay on their sides, and there was little light visible from beneath their bodies. It vanished abruptly with death.

#### STUDY MATERIAL.

A total of 340 specimens was taken, as follows: *Arcturus* Expedition, Station 50 Pt-1(1); 50 Pt-1(1); 53 T-1(3); 56 T-1(6); 59 T-2(4); 59 Pt-1(7); 59 Pt-1(7); 61 T-4(2); 65 Ot-1 and T-3 and T-4(90); 66 T-2(24); 66 Pt-1(20); 66 Pt-1(1); 66 T-2(1); 66 T-2(6); 66 T-3(16); 67 T-1(1); 68 Pt-1(2); 68 Pt-1(5); 74 Pt-3(3); 74 T-22(3); 74 T-26(1); 74 T-42(1); 74 T-69(2); 84 T-10(2); 84 T-14(1); 84 Pt-1(10); 84 Pt-3(1); 84 Pt-4(2); 84 T-19(1); 84 T-20(3); 86 T-4(2); 86 T-7(1); 86 T-8(3); 86 Pt-1(3); 87 T-3(4); 87 Pt-1(6). Eastern Pacific (*Zaca*) Expedition, Station 185 T-1(1); 210 T-1(6); 210 T-2(2); 210 T-3(5); 210 T-6(3); 210 T-6(28); 210 T-7(1); 210 T-7(16); 210 T-8(2); 210 T-10(8); 210 T-10(1); 219 T-1(9); 219 T-2(2); 219 T-2(1); 225 T-1(2); 225 T-1(1); 227 T-1(3); 228 T-1(2); 230 T-1(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII. pp. 6-23 (*Arcturus*); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES AND SYNONYMY.

##### *Lampanyctus omostigma*:

Gilbert, 1908, p. 232, pl. 5. (Type specimen; 62 mm.; also co-type same length; surface; 1,000 miles north of Marquesas). Jordan & Jordan, 1922, p. 12. (Name listed).

Fowler, 1928, p. 68. (Description, synonymy).

Parr, 1928, p. 88. (Key to species).

Parr, 1929, p. 22. (Reexamination of type).

Parr, 1931, pp. 25, 28, fig. 9. (Key to species).

##### *Lampanyctus omostigma parvicauda*:

Parr, 1931, p. 25, fig. 9. (28 specimens, including type and co-type; ? mm.; 100 to 200? fathoms; off western coast Mexico and Nicaragua).

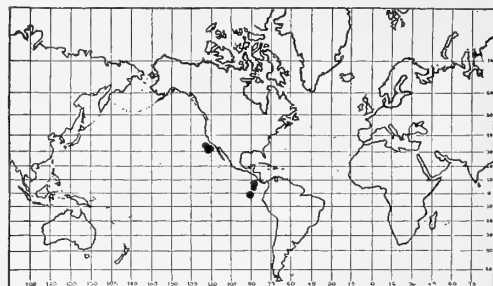
##### *Lampanyctus ritteri* Gilbert, 1915.

*Specimens taken by Eastern Pacific Expeditions:* 19 specimens; *Arcturus* Oceanographic Expedition; 400 to 800 fathoms; between 0° 17' S. and 6° 27' N. Lat., and 85° 00' and 91° 47' W. Long.; lengths 15 to 68 mm.; between May 13 and June 12, 1925.

1 specimen; Eastern Pacific (*Zaca*) Expedition; 500 fathoms; 8° 03' N. Lat., and 83° 12' W. Long., length 45 mm.; March 10, 1938.

*Specimens previously recorded:* 27 specimens; ? to 142 mm.; 350 (?) to 599 fathoms off coast of southern California.

The present paper extends the range of this species about 1,920 miles south to the Galápagos.



TEXT-FIG. 19. Distribution of *Lampanyctus ritteri*.

**Photophore count and variation:** There is considerable variation in the count of anal photophores given by other authors in earlier keys. Gilbert, who described this species, gives 7-8; Bolin 6-8 and 8-9; Parr 8 and 7-8.

Our single (*Zaca*) specimen shows 5-7 on left side, 5-8 on right. The majority of our *Arcturus* fish are slightly mutilated, but the extremes of the countable series are 5-8 and 9-10.

**Food:** The stomach of one fish contained

two euphausiids and one copepod, while another had indulged in two copepods and one euphausiid.

#### STUDY MATERIAL.

A total of 20 specimens was taken, as follows: *Arcturus* Expedition, Station 66 Pt-1(2); 68 T-5(3); 68 Pt-1(3); 74 Pt-1(1); 74 Ot-2(1); 84 Pt-1(1); 84 Pt-3(6); 84 T-8(1); 86 T-10(1). Eastern Pacific (*Zaca*) Expedition Station 219 T-2(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXIII, pp. 287-298 (*Zaca*).

#### REFERENCES.

##### *Lymanayctus ritteri*:

Gilbert, 1915, p. 318, pl. 15, fig. 3. (5 specimens, including type; ? to 142 mm. total length; 350 to 599 fathoms; Monterey Bay, California).

Parr, 1928, p. 89, fig. 24. (Key to species).

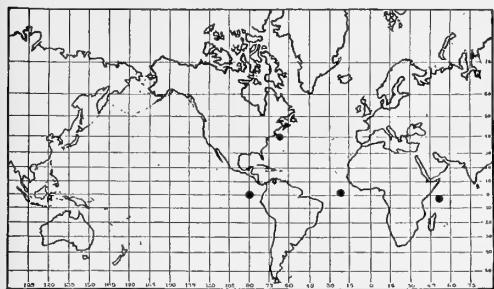
Parr, 1929, p. 23. (Further description).

Bolin, 1939, p. 141, fig. 24. (24 specimens; including 2 co-types; 19.9 to 100.0 mm.; ? fathoms; vicinity San Clemente Island to Point Reyes, California).

##### *Lampanyctus tenuiforme* (Brauer, 1906).

*Specimens taken by Eastern Pacific Expeditions*: 5 specimens; *Arcturus* Oceanographic Expedition; 500 to 700 fathoms; between 0° 17' S. Lat. and 0° 00' equator, and 91° 34' and 91° 53' W. Long.; lengths 24 to 25.5 mm.; June 9 to 13, 1925.

*Specimens previously recorded*: 4 specimens; 16 to 24 mm.; (?) 1,093 to 1,642 fathoms; Hudson Gorge, northwest Atlantic, south Atlantic, Indian Ocean. Our specimens are the first recorded from the eastern Pacific.



TEXT-FIG. 20. Distribution of *Lampanyctus tenuiforme*.

*Photophore variation*: Analysis of our five specimens shows the following arrangements: 6-9, 6-9, 6-10, 7-8, and one with the asymmetrical combination of 6-9, 6-10.

No sex glands are present in our individuals.

#### STUDY MATERIAL.

A total of 5 specimens was taken as fol-

lows: *Arcturus* Expedition, Station 84 Pt-3(3); 84 T-14(1); 87 Pt-1(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

#### REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1928, p. 83).

##### *Myctophum (Lampanyctus) tenuiforme*:

Brauer, 1906, p. 243, fig. 160. (Original description; 1 specimen; 21 mm.; 1,093 fathoms; Indian Ocean).

Pappenheim, 1914, p. 197. (1 specimen; 16 mm.; ? to 1,642 fathoms; south Atlantic).

##### *Lampanyctus tenuiforme*:

Parr, 1928, p. 83. (Key to species; synonymy).

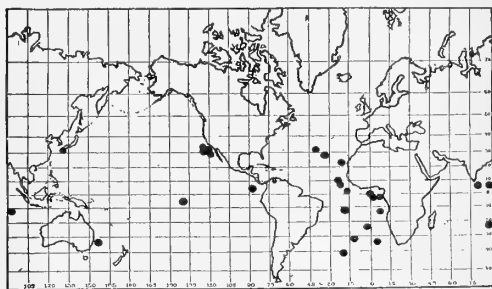
Parr, 1931, p. 28. (Reference).

Beebe, 1929, p. 16. (2 specimens; 18 and 24 mm.; 600 fathoms; Hudson Gorge, northwest Atlantic).

##### *Lampanyctus townsendi* (Eigenmann & Eigenmann, 1889).

*Specimens taken by Eastern Pacific Expeditions*: 1 specimen; *Arcturus* Oceanographic Expedition; 600 fathoms; 6° 24' N. Lat., and 85° 00' W. Long.; length 35 mm.; June 9, 1925.

*Specimens previously recorded*: 43 specimens, ? to 78.5 mm.; surface to 1,367 fathoms; north and south Atlantic Ocean, Indian Ocean, Australia, Japan, mid- and eastern Pacific from southern California to Panama Bay. Our specimen extends the range southward about 2,000 miles.



TEXT-FIG. 21. Distribution of *Lampanyctus townsendi*.

*General data*: Our specimen is badly damaged and torn but all the characters are distinct. It is Cat. No. 5687b, and was taken at Station 66 Pt-1, 130 miles northeast of Cocos Island.

#### STUDY MATERIAL.

One specimen was taken, as follows: *Arcturus* Expedition, Station 66 Pt-1(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

## REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 147).

*Myctophum townsendi*:

Eigenmann & Eigenmann, 1889, p. 125. (Original description; type specimen; ? mm.; 45 fathoms; Cortez Bay, San Diego, California).

*Scopelus (Nyctophus) warmingii*:

Lütken, 1892, p. 259, fig. 19. (Original description; type specimen; 63 mm.; mid-Atlantic).

*Scopelus townsendi*:

Lütken, 1892, p. 267. (This refers to *M. californiense*).

*Lampanyctus warmingii*:

Goode & Bean, 1895, p. 80. (Description).

*Lampanyctus townsendi*:

Jordan & Evermann, 1896, p. 558. (Description).

Gilbert, 1908, p. 230, pl. IV. (1 specimen; 26 mm.; ? to 300 fathoms; Marquesas).

Gilbert, 1913, p. 98. (Key to species; description; 5 specimens; ? to 60 mm.; surface to 850 fathoms; southern Japan).

McCulloch, 1923, p. 115. (1 specimen; 65 mm.; on beach, Lord Howe Island, Australia).

Fowler, 1928, p. 68. (References).

Parr, 1928, p. 79. (Key to species; synonymy).

Parr, 1929, p. 13. (Considers *M. warmingii* after examination of type).

Norman, 1930, p. 327. (14 specimens; 17 to 67 mm.; surface to 1,094 fathoms; north and south Atlantic).

Matsubara, 1938, p. 56, fig. 11. (1 specimen; 78.5 mm.; ? fathoms; Japan).

Bolin, 1939, pp. 93, 147, fig. 28. (Key to species; description; 7 specimens; 17.4 to 57.1 mm.; ? fathoms; coast of California, Japan).

*Myctophum (Lampanyctus) warmingii*:

Brauer, 1906, p. 229. (Key to species; description; 7 specimens; ? to 21 mm.; surface to 1,367 fathoms; Gulf of Guinea, Indian Ocean, Bay of Bengal, south of Japan).

Pappenheim, 1914, p. 195. (5 specimens; 19 to 36 mm.; ? to 3,000 metres wire; mid- and south Atlantic).

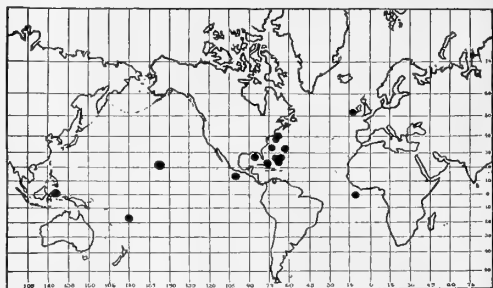
*Myctophum (Lampanyctus) townsendi*:

Brauer, 1906, p. 167. (Key to species).

*Diaphus dumerili* (Bleeker, 1856).

*Specimens taken by Eastern Pacific Expeditions*: 3 specimens; Eastern Pacific (*Zaca*) Expedition; surface; at 16° 30' N. Lat., and 99° 13' W. Long.; lengths 53, 54 and 64 mm.; Nov. 29, 1937.

*Specimens previously recorded*: 65 specimens; ? to 95 mm.; surface to (?) 800 fathoms; northwest Atlantic, Bermuda, Bahamas, West Indies, Gulf of Mexico, southwest of Ireland, south Atlantic, Fiji Islands, Hawaii and Celebes.



TEXT-FIG. 22. Distribution of *Diaphus dumerili*.

*Photophore variation*: Two fish showed the combination of 7-5, while the third presented the asymmetrical formula of 7-6, 6-6.

## STUDY MATERIAL.

A total of 3 specimens was taken, as follows: Eastern Pacific (*Zaca*) Expedition, Station 190 L(3). For detailed trawling data, refer to *Zoologica*, Vol. XXIII, pp. 287-298.

## REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1928, p. 126).

*Scopelus dumerili*:

Bleeker, 1856, vol. 1, p. 66. (Description and type locality, Manado, Celebes).

Günther, 1864, vol. 22, p. 410. (Brief description).

Günther, 1887, p. 198. (Description; 1 specimen; 76 mm.; 315 fathoms; Fiji Islands).

*Scopelus schmitzi*:

Johnson, 1890, p. ? (Reference not seen; synonymized by Tåning, 1928, p. 58).

*Myctophum nocturnum*:

Poey, 1860, p. 416. (Brief description; 1 specimen; 95 mm.; ? fathoms; ? locality).

*Myctophum (Nyctophus) lacerta*:

Brauer, 1904, p. 392. (Key to species).

*Collettia nocturna*:

Jordan & Evermann, 1896, p. 567. (Description).

*Diaphus nocturnus*:

Gilbert, 1906, p. 255. (Detailed description of types and co-types).

*Myctophum dumerili*:

Weber & Beaufort, 1913, p. 670. (Brief reference).



*Lampanyctus lacerta*:

Goode & Bean, 1895, p. 81, fig. 89. (Type description; 3 specimens; ? to 57 mm.; surface to 671 fathoms; northwest Atlantic, Gulf of Mexico).

Jordan & Evermann, 1896, p. 560. (Brief description).

Breder, 1927, p. 17. (Brief description; ? specimens; 50 mm.; ? fathoms; West Indies).

*Diaphus dumerili nocturnus*:

Tåning, 1928, p. 58. (Key to species).

*Diaphus dumerili*:

Fowler, 1928, p. 68. (Brief description; synonymy; 1 specimen; ? mm.; ? fathoms; Hawaii).

Parr, 1928, pp. 115, 126-130, fig. 23. (Key to species; synonymy; detailed description and discussion; 47 specimens; ? to 73 mm.; surface to 800 fathoms; San Salvador and Acklin Islands, in the Bahamas).

Parr, 1929, pp. 29, 31. (Key to species; synonymy).

Parr, 1934, p. 48. (Synonymy).

Norman, 1929, p. 511. (1 specimen; 53 mm.; ? fathoms; off southwest Ireland).

Norman, 1930, p. 331. (1 specimen; 47 mm.; 54 to 108 fathoms; south Atlantic).

Borodin, 1931, p. 76. (? specimens; ? mm.; ? fathoms; near Bermuda).

Fraser-Brunner, 1935, p. 319. (Name listed).

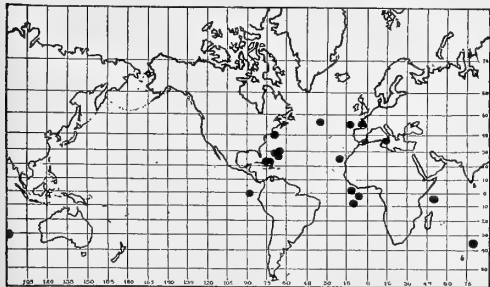
Beebe, 1929, p. 15. (2 specimens; ? mm.; ? fathoms; Hudson Gorge, northwest Atlantic).

Beebe, 1937, p. 204. (Preliminary list; 7 specimens; 54 to 66 mm.; surface; Bermuda).

*Diaphus gemellari* (Cocco, 1838).

*Specimens taken by Eastern Pacific Expeditions*: 1 specimen; *Arcturus* Oceanographic Expedition; 700 fathoms; between 0° 40' N. Lat., and 88° 51' W. Long.; length 33 mm.; April 3, 1925.

*Specimens previously recorded*: 61 specimens; ? to 86 mm.; surface to 1,000 fathoms; northwest Atlantic, Bermuda, Bahamas, West Indies, Canary Islands, Mediterranean, Indian Ocean.



TEXT-FIG. 23. Distribution of *Diaphus gemellari*.

*Photophore count*: Our specimen shows 5-6, 5-6.

## STUDY MATERIAL.

One specimen was taken as follows: *Arcturus* Expedition, Station 33 Pt-1(1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23.

## REFERENCES AND SYNONYMY.

(Synonymy accepted according to Parr, 1928, p. 123).

*Nyctophus gemellarii*:

Cocco, 1838, p. ? (Reference not seen).

*Scopelus gemellarii*:

Cuvier & Valenciennes, 1828-49, p. 445. (Brief description).

Günther, 1864, V. 22, p. 415. (Description).

Canestrini, 1870, p. ? (Reference not seen).

Doderlein, 1878-79, p. 54. (Name listed).

Giglioli, 1880, p. ? (Reference not seen).

Vaillant, 1888, p. 117. (Description; 6 specimens; ? mm.; 550 to 1,200 fathoms; Canary Islands, Messina, coast of Morocco).

Raffaele, 1889, p. 183, fig. 8. (Brief description).

Carus, 1889-93, p. 564. (Description).

*Scopelus uraeoclampus*:

Facciola, 1882-83, p. 50. (Description of type; Messina).

*Scopelus (Nyctophus) gemellarii*:

Lütken, 1892b, p. 260. (Description).

*Myctophum gemellarii*:

Bonaparte, 1832-41, V. 3, Fasc. 27, fig. 2. (Detailed description).

Sanzo, 1918a, p. 9. (Description; 8 specimens; 3 to 17 mm.; ? fathoms; Mediterranean).

*Myctophum (Nyctophus) gemellarii*:

Brauer, 1904, p. 393. (Key to species).

*Lampanyctus gemellarii*:

Goode & Bean, 1895, p. 80. (Description and synonymy).

*Myctophum (Diaphus) gemellari*:

Brauer, 1906, pp. 164, 212, figs. 130, 131. (Description; key to species; synonymy; 5 specimens; 12 to 18 mm.; ? fathoms; Messina).

Fage, 1910, p. 13, pl. 1, fig. 7. (Description; 1 specimen; 32 mm.; 500 fathoms; Mediterranean).

Zugmayer, 1911b, p. 29. (Description; synonymy; 1 specimen; 30 mm.; ? fathoms; Mediterranean, Atlantic and Indian Ocean).

*Diaphus gemellari*:

Tåning, 1918, p. 73. (Description; development; 78 specimens; 5 to 24 mm.; surface to 55 fathoms; Mediterranean).

Tåning, 1928, p. 58. (Key to species).  
Parr, 1928, pp. 115, 123-125, figs. 21, 22. (Key to species; synonymy; detailed description; 5 specimens; ? to 45 mm.; 5 to 8,000 feet wire; Bahamas, Bermuda).

Parr, 1929, p. 29. (Key to species).

Parr, 1934, p. 64. (Description; 2 specimens; 37 and 67 mm.; 600 fathoms; north Atlantic).

LeGendre, 1934, p. 340. (Key to species; 2 specimens 1 male, 1 female; 83 and 86 mm.; ? fathoms; Gulf of Gascony).

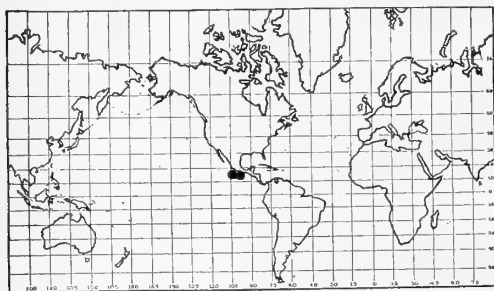
Beebe, 1929, p. 15. (3 specimens; ? mm.; ? fathoms; Hudson Gorge, north Atlantic).

Beebe, 1937, p. 204. (Preliminary list; 27 specimens; 10 to 28 mm.; 300 to 1,000 fathoms; Bermuda).

#### *Diaphus pacificus* (Parr, 1931).

*Specimens taken by Eastern Pacific Expeditions:* 19 specimens; Eastern Pacific (Zaca) Expedition: 300 to 400 fathoms; at 17° 45' N. Lat., and 103° 05' W. Long.; lengths 24 to 30 mm.; November 23, 1937.

*Specimens previously recorded:* 1 specimen; 28 mm.; 625 fathoms cable; eastern Pacific coast of Mexico.



TEXT-FIG. 24. Distribution of *Diaphus pacificus*.

*Photophore count and variation:* In general 5-4 on both left and right side; several were 4-4 on both sides, and one was 5-3. Asymmetrical combinations were 5-4 and 4-4, 4-5 and 5-4 and a third showed 5-3, and 4-5.

#### STUDY MATERIAL.

A total of 19 specimens was taken, as follows: Eastern Pacific (Zaca) Expedition, Station 185 T-1 (13), 185 T-2 (6). For detailed trawling data, refer to *Zoologica*, Vol. XXIII, pp. 287-298.

#### REFERENCES AND SYNONYMY.

##### *Diaphus pacificus*:

Parr, 1931, p. 34, fig. 14. (Description of type specimen; 28 mm.; 625 fathoms cable; eastern Pacific, off coast of Mexico).

##### *Diaphus rafinesquii* (Cocco, 1838).

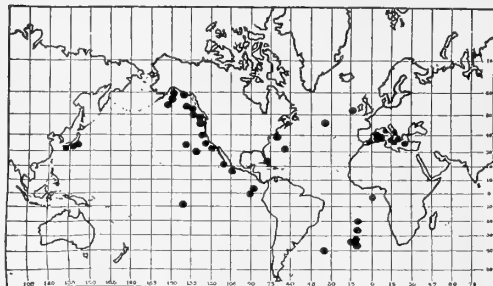
*Specimens taken by Eastern Pacific Expeditions:* 19 specimens; *Arcturus* Oceano-

graphic Expedition; 300 to 1,000 fathoms; between 0° 17' S. and 4° 50' N. Lat., and 86° 43' and 91° 53' W. Long.; lengths 11 to 39 mm.; between May 1 and June 13, 1925.

4 specimens; Templeton Crocker Expedition; 400 to 500 fathoms; at 23° 25' N. Lat., and 108° 31' W. Long.; lengths 15 to 27 mm.; April 29, 1936.

1 specimen; Eastern Pacific (Zaca) Expedition; 500 fathoms; at 17° 45' N. Lat., and 103° 05' W. Long.; Nov. 23, 1937.

*Specimens previously recorded:* 1,032 specimens; ? to 90 mm.; surface to 1,000 fathoms; north and south Atlantic; Mediterranean, Japan, mid-Pacific, eastern Pacific from Sitka, Alaska down to San Diego, California.



TEXT-FIG. 25. Distribution of *Diaphus rafinesquii*.

*Photophore variation:* There were five symmetrical combinations in 22 specimens; one was 4-4; eleven were 5-4; two were 5-3; three were 6-3; and five were 6-4. Two fish had the asymmetrical combinations of 4-5, 5-4, and 5-4, 4-4. One of these asymmetrical specimens, (Cat. No. 5571) had the characteristics of *D. holti* on one side.

*Vertical distribution:* If anything of value can be deduced from the vertical distribution of 24 fish, it is that almost half were taken at 500 fathoms. The exact data is: 300 fathoms (2 fish), 400 (7), 500 (11), 600 (1), 700 (2) and 1,000 fathoms (1 fish).

*Sociability:* Nothing definite. Eight nets contained one fish each, five nets two, and one net six fish.

#### STUDY MATERIAL.

A total of 24 specimens was taken, as follows: *Arcturus* Expedition, Station 59 T-3 (2); 74 T-78 (1); 84 T-20 (2); 86 T-1 (1); 86 T-2 (6); 86 T-7 (1); 86 T-9 (1); 86 T-11 (1); 87 T-2 (1); 87 T-3 (2); 87 T-6 (1). Templeton Crocker Expedition, Station 158 T-3 (2); 158 T-4 (2). Eastern Pacific (Zaca) Expedition, Station 185 T-3 (1). For detailed trawling data, refer to *Zoologica*, Vol. VIII, pp. 6-23 (*Arcturus*); Vol. XXII, pp. 37-46 (Templeton Crocker); Vol. XXIII, pp. 287-298 (Zaca).



## REFERENCES AND SYNONYMY.

(Synonymy accepted according to Bolin, 1939, p. 125).

*Nyctophus rafinesquii*:

Cocco, 1838, p. 20, pl. 3, fig. 7. (Original description; reference not seen).

*Myctophum rafinesquei*:

Bonaparte, 1832-1841, V. 3, Fasc. 27, fig. 2. (Description).

Sanzo, 1918a, p. 5. (Discussion).

*Scopelus rafinesquii*:

Cuvier & Valenciennes, 1828-1849, vol. 22, pp. 330, 444. (Brief description).

Günther, 1864, vol. 22, p. 410. (Description of Mediterranean fish).

Giglioli, 1880, p. ? (Reference not seen).

Doderlein, 1878-79, p. 54. (Name listed).

Canestrini, 1870, p. 125. (Reference not seen).

Leydig, 1881, p. ? (Reference not seen).

Raffaele, 1889, p. 183. (Brief description; 13 specimens; ? mm.; ? fathoms; Messina).

Carus, 1889-1893, p. 564. (Description).

Moreau, 1891, p. 98. (Detailed description and synonymy).

Holt & Byrne, 1910, p. 22, fig. 6. (Description; 1 specimen; 75 mm.; 730 fathoms; southwest coast of Ireland).

*Scopelus rafinesque*:

Weill, 1926, p. 472. (Brief discussion of luminosity).

*Scopelus (Nyctophus) rafinesquii*:

Lütken, 1892, p. 258, fig. 17. (Description; 3 specimens; 43, 64 and 90 mm.; ? fathoms; ? locality).

*Scopelus protocus*:

Lütken, 1892, p. 266. (Reference).

*Myctophum protocus*:

Gilbert, 1890, p. 52. (Description of type; 3 specimens; ? mm.; 584 fathoms; off Cape Johnson, Washington).

Parr, 1929, p. 32. (Discussion of synonymy).

*Myctophum (Nyctophus) rafinesquii*:

Brauer, 1904, p. 393. (Key to species; synonymy).

*Myctophum (Nyctophus) theta*:

Brauer, 1904, p. 393. (Key to species).

*Myctophum (Diaphus) theta*:

Brauer, 1906, p. 165. (Key to species).

*Diaphus theta*:

Eigenmann & Eigenmann, 1890, p. 4. (11 specimens from the mouths of rock cod, Point Loma, California).

Evermann & Goldsborough, 1906, p. 271. (1 specimen; 57 mm.; 922 fathoms; Sitka, Alaska).

*Diaphus nanus*:

Gilbert, 1908, p. 224, pl. 1. (Type description; 1 specimen; 17 mm.; surface to 300 fathoms; Marquesas).

Gilbert, 1913, p. 87. (Description; ? specimens; ? 45 mm.; ? 300 fathoms; Japan).

*Diaphus holti*:

Tåning, 1918, pp. 88-92, figs. 35, 36. (Detailed description; distribution map; 638 specimens; 275 to 550 fathoms; near Messina, Mediterranean and Bay of Cadiz).

*Diaphus mollis*:

Tåning, 1928, p. 60. (Preliminary type description; key to species).

*Collettia rafinesquei*:

Goode & Bean, 1896, p. 88, pl. 26, fig. 100. (Description; synonymy; 3 specimens; ? to 77 mm.; northwest Atlantic).

Jordan & Evermann, 1896, p. 567. (Description).

*Myctophum (Diaphus) rafinesquei*:

Brauer, 1906, pp. 165, 223, figs. 144, 145. (Key to species; description; synonymy; 25 specimens; ? to 66 mm.; ? fathoms; Messina).

Zugmayer, 1911, p. 32. (Synonymy; 2 specimens; ? to 30 mm.; ? fathoms; Mediterranean).

*Diaphus rafinesquii*:

Tåning, 1918, pp. 83-87, figs. 33, 34. (Detailed description; distribution map; 123 specimens; surface to 1,093 fathoms; Mediterranean).

Tåning, 1928, p. 60. (Key to species).

Parr, 1928, pp. 119, 131-135, figs. 25, 26. (Key to species; synonymy; detailed discussion; 4 specimens; 38 to 46 mm.; 7 to 10,000 feet wire; Bahamas, Bermuda).

Parr, 1929, p. 32, fig. 16. (Key to species; synonymy; detailed discussion and description).

Parr, 1934, pp. 51, 65. (Reference to type in poor condition; also 1 specimen; ? mm.; 600 fathoms; mid-north Atlantic).

Norman, 1930, p. 334. (References; brief discussion; 27 specimens; 16 to 70 mm.; ? fathoms; south Atlantic).

LeGendre, 1934, p. 341. (Key to species).

Beebe, 1937, p. 203. (Preliminary list; 134 specimens; 9 to 70 mm.; 400 to 1,000 fathoms; Bermuda).

Bolin, 1939, pp. 93, 125, fig. 18. (Key to species; synonymy; detailed description; 23 specimens, including 4 co-types 11 to 65.6 mm.; ? fathoms; from mid-Washington to southern California, Japan, Messina).

Chapman, 1940, p. 33. (Description; 22 specimens; 45 to 73 mm.; ? to 850 metres wire; eastern Pacific between Alaska and British Columbia).

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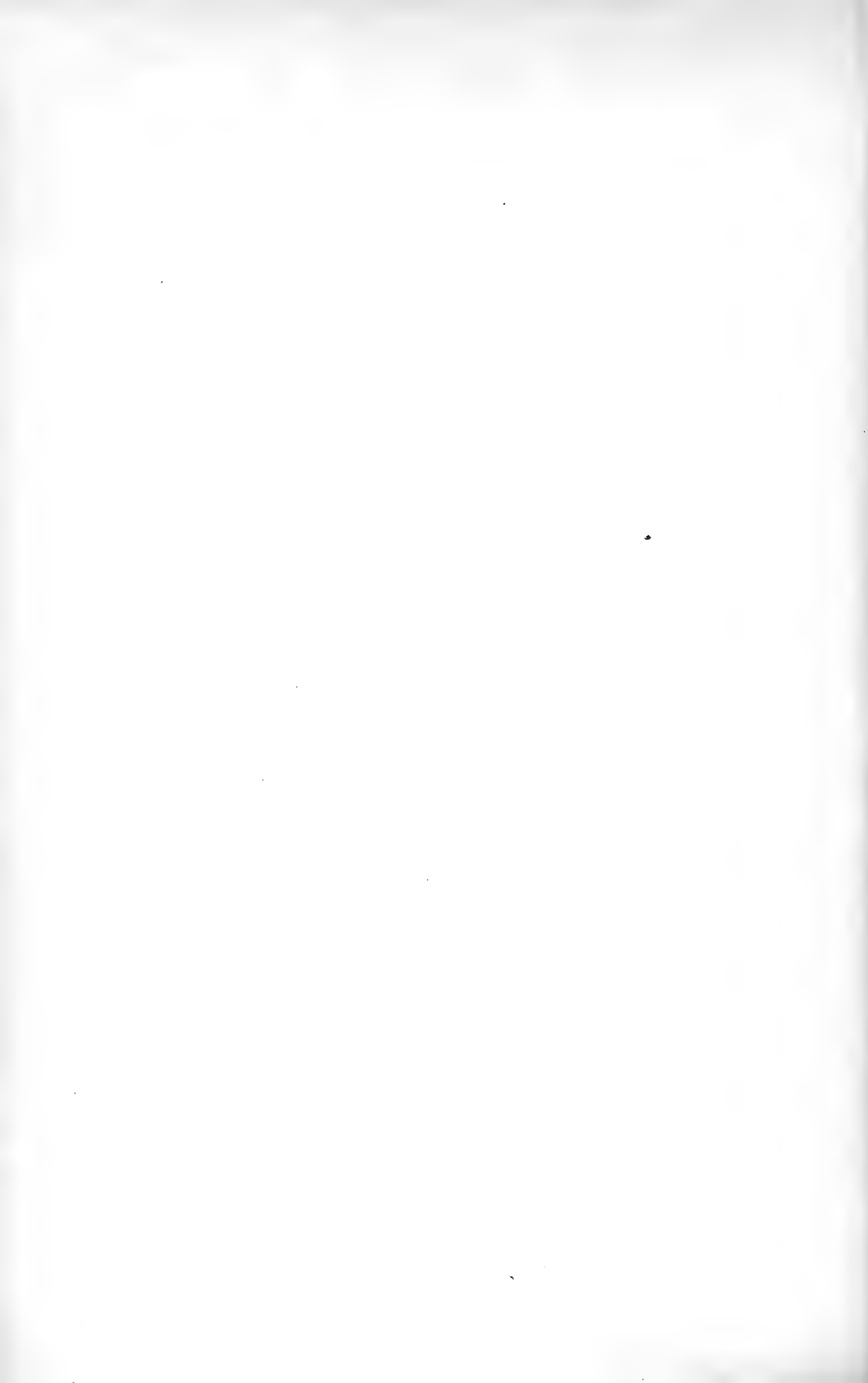
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## 10.

The Psammocharidae (Hymenoptera) Taken at Kartabo  
and Other Localities in British Guiana.<sup>1</sup>

NATHAN BANKS.

[During the eight years of occupancy, by the Department of Tropical Research, of the New York Zoological Society's Station at Kartabo, British Guiana, extensive collections of insects were made. Most of these were taken in the quarter-mile area under intensive study—what may be called the Guiana Junglezone. Details and a general summary of this area may be found in "Studies of a Tropical Jungle," *Zoologica*, Vol. VI, No. 1.]

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## INTRODUCTION.

During his trips to the Tropical Research Laboratory of the New York Zoological Society at Kartabo, British Guiana, Dr. William Beebe collected many specimens of Psammocharidae. These, together with specimens from Cornell University and those in the Museum of Comparative Zoology, form the basis of this paper.

There are but few records of these insects from this country. In 1848 W. F. Erichson published seven species in Schomburgk's *Reise in Guiana*; in 1913 Peter Cameron recorded or described 23 species in the *Jr. R. Agric. Soc. of Demerara*—and in 1928 F. X. Williams in his *Studies in Tropical Wasps* recorded three species. Many of the species described by Fabricius from "Amer. merid." were probably from this general region. In the revision of the genus *Pepsis* by Lucas in 1895, there are hardly any records except those of Erichson. Since so

<sup>1</sup>Contribution No. 692, Department of Tropical Research, New York Zoological Society.

little has been published and much of it many years ago it is evident that there will be many new genera as well as species.

In this paper 86 species are recorded; two of Cameron have not been identified. This is probably not half that occur in British Guiana. Fifteen species appear to be new, several in new genera. But one species, *Notiochares amethystina*, is widely distributed in tropical South America, but nearly all the previously described species are known from localities in northern South America and Brazil; several are also known from Peru and Bolivia, almost none from Paraguay or Argentina. Two, *Pepsis ruficornis* and *Priochilus opacifrons*, are recorded from the West Indies.

In 1897 William Fox described the Brazilian species collected by H. H. Smith; this work has been most useful to me, and three years ago I studied this collection in the Carnegie Museum, made many notes thereon, synoptic tables of the species, and comparisons with the types.

The material sent by Dr. Beebe was taken mostly at the Tropical Research Laboratory at Kartabo, but other specimens are from the Penal Settlement, Kaieteur, Kalacoon, Kangaruma, Arakaka, Mt. Everard, Georgetown, and west bank of the Demerara River.

The Cornell material from British Guiana is mostly from Bartica, but many from Demerara River, others from Kartabo, Kaieteur, Penal Settlement, Georgetown, Tumatumari on Potaro River, and Rockstone, Essequibo River, mostly taken by H. L. Parish, others by Prof. Forbes and Dr. Babi. The Museum of Comparative Zoology material is chiefly from Kartabo, taken by Dr. W. M. Wheeler, others from Bartica. H. Lang took specimens at Kamakusa and Georgetown which were presented by Dr. J. Bequaert. Dr. N. A. Weber gave a number captured at a Forest Settlement on the Mazaruni River, and from J. Ogilvie a few were obtained taken at the source of the Essequibo River.

#### SYNOPSIS OF THE SUBFAMILIES.

1. Labrum wholly exposed, and often as long as the clypeus; no hairs or bristles on the basal parts of maxillae; no groove on second ventral segment; no separated hind border to the propodeum. In the fore wing the first recurrent vein ends beyond the basal third of second submarginal cell and no pocket in base of second discoidal cell; in hind wing the anal vein ends before the origin of the radial sector. Legs with very small short spines, hind tibiae never with teeth or carina above; claws cleft..... 2  
Labrum partly hidden under clypeus,

- if (some *Pepsis*) it is wholly visible, then the first recurrent vein ends before end of basal third of second submarginal cell and the anal in hind wing ends as far out as origin of radial sector..... 3
2. Inner margin of eyes emarginate above middle; face much narrowed below; propodeal spiracle about its length from the base of propodeum; often spines on under side of last joint of mid- and hind tarsi..... *Ceratopalinæ*  
Inner margin of eyes not emarginate; face but little narrowed below; propodeal spiracle twice its length from the base of propodeum; no spines on under side of last joint of mid- and hind tarsi ..... *Notocyphinae*
3. In fore wing first recurrent vein ends before end of basal third of second submarginal cell, and in hind wing the anal vein ends as far out as origin of radial sector; basal parts of maxillae and the mentum lack hairs or bristles; second ventral segment in females at least with a transverse groove; hind tibia of female spined and toothed above; hind basitarsus of male compressed; claws never cleft; under side of last joint of mid- and hind tarsi with lateral spines (at least in female) ..... *Pepsinae*  
In fore wing the first recurrent vein ends beyond the basal third of second submarginal cell, (exceptions rare), and in hind wing the anal ends before the origin of the radial sector; basal parts of the maxillae or the mentum usually with hairs or bristles..... 4
4. No pocket in base of second discoidal cell; second ventral segment, at least in female, with a transverse groove or impression; last joint of mid- and hind tarsi sometimes with lateral spines; spines at tip of the hind tibia if noticeable are short and nearly parallel.... 5  
A pocket in base of second discoidal cell; no groove on second ventral segment; hind tibia never with teeth or a carina above; spines at tip of hind tibia moderately long and inner one divergent; usually minute spine-pits above on hind femora near its tip; last joint of mid- and hind tarsi may have median spines below but not lateral ones; female sometimes with a comb on front tarsi; claws toothed or cleft; a separated hind border to propodeum ..... *Psammocharinae*
5. Last joint of mid- and hind tarsus often with spines below, usually lateral; hind tibia often toothed above or with a carina; claws toothed or cleft; hind basitarsus of male not compressed;

base of abdomen rather flat at connection with propodeum, the first segment may be tapering, but not petiolate ..... *Cryptochilinae*

Last joint of hind tarsus usually bare beneath, rarely weak spines or bristles; claws never cleft; hind tibia never with teeth above or a carina, legs rarely hairy or bristly; no spine-pits on hind femora; abdomen attached by a distinct petiole ..... *Pseudageninae*

The subfamily Ceratopalinae was not represented in the collection.

### PEPSINAE.

At present this includes but one genus, *Pepsis*, although it will be divided into several in the future.

### SYNOPSIS OF *Pepsis*.

1. Wings entirely deep black, without even a pale margin ..... 2
- Wings not entirely deep black, a pale margin or bands, or mostly rufous or brown ..... 14
2. Antennae black, at most the extreme tip sometimes rufous ..... 3
- Antennae with at least several apical joints rufous or yellowish ..... 6
3. Propodeum very hairy and at the turn from basal to apical part with a crest of dense shaggy hair; wings not especially iridescent; mesosternal tubercle some distance from mid-coxal slope ..... *elevata*
- Propodeum without a crest of shaggy hair; mesosternal tubercle at beginning of mid-coxal slope; wings plainly iridescent ..... 4
4. Wings beautifully iridescent violet to reddish, changing to bluish near tips and greenish in places; male with middle of fourth ventral with erect hairs denser on sides and with incurving tips ..... *margarete*
- Wings iridescent bluish ..... 5
5. Male with a large patch of long, erect hair on middle of fourth ventral segment ..... *fulgidipennis*
- Male with middle of fourth and most of fifth ventral segment smooth and shining, but on each side a dense row of incurving hairs ..... *nireus*
6. Antennae rufous or yellowish from base of third joint to tip ..... 7
- Antennae rufous from tip of third joint or beyond; mid-ridge of propodeum low or absent ..... 11
7. Antennae pale yellow ..... 8
- Antennae rufous or orange-red ..... 9
8. Male with a row of hairs on each side of posterior part of fourth segment ..... *luteicornis*
- Male with a few hairs on each side of anterior part of fourth segment ..... *flavicornis*
9. Body extremely hairy above and below, except above on abdomen; especially long on propodeum; clypeus with long hairs on basal part as well as apical ..... *xanthocerus*
- Body but little hairy, on clypeus only on lower part ..... 10
10. Propodeum with considerable long hair; teeth on hind tibia above well separated and tips rather blunt ..... *ruficornis*
- Propodeum scarcely at all hairy above; teeth on hind tibia above pointed and but little separated ..... *excelsa*
11. Rufous begins on the fourth or fifth joint; wings often hardly deep black ..... 12
- Rufous begins on the sixth, seventh or eighth joint. Wings somewhat brownish ..... 13
12. Basal and apical parts of propodeum plainly separated by a low mid-ridge; wings with a bluish to violet iridescence; length of fore wing about 30 millimeters; tibial teeth rather small ..... *ianthina*
- Basal and apical parts of propodeum not separated, no mid-ridge; wings not iridescent; fore wing about 20 millimeters long; teeth on hind tibia very small ..... *vicina*
13. No distinct mid-ridge on propodeum; five or six joints of antennae pale; third cubital cell little longer than broad ..... *sagana*
- A low but distinct mid-ridge on propodeum; four joints of antennae pale; third cubital cell much longer than broad ..... *diabolus*
14. Wings almost wholly rufous or yellowish-red, no broad dark border; antennae almost wholly rufous ..... 15
- Wings with at least about half brown or black ..... 18
15. Head and thorax with golden pubescence; mesosternal tubercle some distance before the mid-coxal slope ..... *plutus*
- No golden hair; mesosternal tubercle usually at coxal slope ..... 16
16. Head with very high vertex, and back of eyes is longer than width of an eye; labrum often wholly visible ..... *frivaldszkyi*
- Head not extended back of eyes to any such extent; vertex normal ..... 17
17. Fore wings with darkened apical border ..... *hecate*

Fore wings not darkened apically....

- ..... *gracilis*
18. Almost apical half of wing yellowish, basal part black; antennae black; teeth on hind tibia very small..... *strenua*  
Apical half not yellowish..... 19
19. Wings wholly brown or blackish-brown ..... 20  
Wings mostly black, but with some yellowish, rufous, white or hyaline..... 21
20. Wings brown to dark brown, about nine joints of antennae pale; a low but distinct mid-ridge ..... *niphe*  
Wings blackish-brown; no mid-ridge ..... no. 12, 13
21. Antennae black; fore wing marked with hyaline or white at tip or base. 22  
Antennae partly rufous, two to six joints; wings yellowish on basal part ..... 25
22. White at base of wings, and tips narrowly ..... *equestris*  
No white at base of wings..... 23
23. A broad white apical band, fully one-fourth length of wing..... *pretiosa*  
A narrow apical border hyaline or whitish ..... 24
24. At tip of both fore and hind wings; mid-ridge high ..... *grossa*  
A spot at tip only on hind wings; mid-ridge very low..... *lucunda*
25. The yellowish band separated from base by an equally broad black band; five or six joints of antennae pale ..... *completa*  
The yellowish occupying basal half of both fore and hind wings, scarcely any black before it..... 26
26. Antennae with five or six joints rufous; not over one-half of wings yellowish; male with a brush on tip of fourth ventral segment..... *dimidiata*  
Antennae with but two or three joints pale; about three-fourths of wing yellowish, male with a tuft of hairs with incurved tips on each side of fourth ventral segment ..... *festiva*

### PEPSINAE.

#### *Pepsis frivaldszkyi* Mocz.

One from sources of Rio Essequibo (J. Ogilvie). Also recorded from Para, Brazil.

This species has the vertex raised and the head extended back of eyes, and the lip is wholly visible, about as in *Notocyphus*; mesosternum densely long-haired; mesosternal tubercle a little before the coxal slope, low and broad, hind tibia has small triangular teeth, well separated, the spines scarcely if any longer than teeth, but the slightly curved bristles are longer.

#### *Pepsis strenua* Erichs.

From Kartabo, March 1; Georgetown, February 15; Forest Settlement, Mazaruni River, August.

The mesosternal tubercle is at base of coxal slope, broad and low.

#### *Pepsis plutus* Erichs.

Penal Settlement, No. Hym. 287; Kartabo, March 3, June 30; Forest Settlement, Mazaruni River, August-September. Also recorded from Para, Brazil.

Mesosternal tubercle about at middle of mesosternum, long before coxal slope.

#### *Pepsis grossa* Fabr.

One from Kalacoon, No. Hym. 43. Also recorded from Colombia and Brazil. Mesosternal tubercle a little more than half way to end of mesosternum, fairly large.

#### *Pepsis elevata* Fabr.

Kartabo, January 23, June 13. No. Hym. 256. Also recorded from Cayenne and Brazil.

Mesosternal tubercle at about one-third the length of mesosternum before tip, rather large.

#### *Pepsis fulgidipennis* Mocz.

Bartica, August 17, June 11; Kartabo, No. 20,136; Arakaka, December 21. Also recorded from Colombia, Venezuela, Surinam and Brazil.

Mesosternal tubercle at base of coxal slope, but this is very short; prominent and almost visible from above.

#### *Pepsis margarete* Lucas.

Arakaka, December 20, 21 (mostly males); Waratuk, February 16. Also recorded from Panama, Colombia, Venezuela and Brazil and Kartabo.

Mesosternal tubercle near coxal slope, not prominent.

#### *Pepsis niphe* Mocz.

One female from Kartabo, May 8. Also recorded from Obydos, Brazil.

Mesosternal tubercle at base of coxal slope.

#### *Pepsis excelsa* Lucas.

Kartabo, March 1, June 30, October 8, No. 201255; Arakaka, December 20; Georgetown, February 15; Demerara River, January 5; Bartica; Kalacoon No. 52; Penal Settlement, No. Hym. 226, September 20; and Rio Mazaruni, August. Also recorded from Brazil.

The mesosternal hump is visible from above, and near coxal slope the teeth on hind tibia are large, sharp pointed, and rather close together, quite different from the widely separated, smaller teeth in *P. ruficornis*.

***Pepsis xanthocerus* Dahlb.**

From Kartabo, May 22, July; Bartica, April 15, May 20; Kaieteur, August 4; Upper Essequibo River (Rucker & Romitti), February 24. Also recorded from Brazil.

The mesosternal tubercle is situate near the coxal slope. It is quite possible that this is the *ruficornis* of Fabricius rather than the form called *ruficornis* by Lucas.

A male from Mackenzie, Demerara River, June 22 (Cornell), is probably this species. It is black, antennae rufous from base of second flagellar joint, venation similar to female, but the third submarginal cell a little shorter. Head, thorax and propodeum very hairy as in the female. The tibia and tarsus of hind leg are compressed and fringed, the basitarsus more than in *luteicornis*. On the middle of the fourth ventral segment is a mass of erect, fairly long hair, leaving the extreme hind border of segment smooth; on the hind part of the fifth ventrite is a row (two or three deep) of erect hairs, about one-half as long as those on the fourth, hardly dense enough to be a "comb," and with fewer hairs in the middle; subgenital plate rather short and broadly rounded at tip, its apical half with fine, dense appressed pubescence.

***Pepsis ruficornis* Fabr.**

Females from Kartabo, May 3, 6, April 20. Also recorded from Cuba, Haiti, Porto Rico, Honduras, Colombia and Cayenne.

Mesosternal tubercle near coxal slope.

***Pepsis luteicornis* Fabr.**

Kartabo, March 11, May 27, June 14, July-August, No. 130,179; Arakaka, December 21, and West bank Demerara River, February 9; all males. Also recorded from Colombia, Surinam and Brazil.

***Pepsis flavicornis* Moc.**

One male from Kamakusa. Also recorded from Brazil.

***Pepsis ianthina* Erichs.**

Kartabo, June 5, July 8, August 6; Bartica, December 23. Also recorded from Panama, Surinam and Brazil.

Mesosternal tubercle a little before coxal slope, elevated, prominent, and projects a little laterally.

***Pepsis sagana* Lucas.**

Kartabo, January 11, March 23, summer of 1923, No. 21104. Also recorded from Brazil.

Mesosternal tubercle placed laterally at base of coxal slope, prominent.

***Pepsis vicina* Lucas.**

Kartabo, May 28, April 14. Also recorded from Surinam.

Mesosternal tubercle near coxal slope, but

not as lateral as in *P. sagana*. The teeth on hind tibia are very small, much smaller than in *sagana*.

***Pepsis iucunda* Lucas.**

From Kartabo, July 21, and October; Forest Settlement, Mazaruni River, August-September. Also recorded from Surinam.

The male has the tip of hind wings pale as in female; the fourth ventrite has on each side an oblique, rather dense row of hairs curving toward each other, the enclosed area smooth behind, punctate in front and with some short erect hairs; fifth segment punctate, more densely so on sides and with erect hair most noticeable on sides. Subgenital plate rather short, rounded at tip, with some fine hair on surface.

***Pepsis dimidiata* Fabr.**

Kangaruma, February 15; Kaieteur, February 18, March 24, and Bartica District.

All of the specimens seen from British Guiana as well as those from French Guiana and Surinam have the yellowish band scarcely beyond the hyaline spot of second discoidal cell, while those from Colombia have this band extending plainly beyond the hyaline spot; the hair brushes of males are the same. The mesosternal tubercle prominent, tip rounded, situate at base of coxal slope, projects a little laterally. Also recorded from Panama, Colombia and Brazil.

***Pepsis completa* Sm.**

From Kalacoon, No. 227. Also recorded from Brazil.

Mesosternal tubercle small, at base of coxal slope, projecting somewhat laterally.

***Pepsis pretiosa* Dahlb.**

Kartabo, one male, No. 131. Also recorded from Caracas, Venezuela and Brazil.

***Pepsis equestris* Erichs.**

Described from British Guiana; have seen none in these collections but many from Colombia, Trinidad and Brazil.

***Pepsis diabolus* Lucas?**

A female from Kartabo, May 24, runs to this in the Lucas tables but does not agree very well with description. Also recorded from Brazil.

***Pepsis* sp. near *ruficornis*.**

Female from Kartabo, June 7.

In size and appearance much like *P. ruficornis*; however, there is a pale yellowish area in hind wing from end of basal fourth to little beyond middle; the antennae are rufous from base of fourth joint; on the propodeum the striae are fairly even and rather numerous; a small mid-ridge, and small lateral tubercles; the mesosternal tubercle at base of coxal slope, rather large, and projecting somewhat laterally. On hind

tibia the teeth are larger than in *ruficornis*, triangular, and closer together. The color is a brighter blue than *ruficornis*.

***Pepsis hecate* Moc.**

A female from Tumatumari, Potaro River, June 28. Also recorded from Brazil.

Mesosternal tubercle of good size, at base of slope, but the slope is longer than usual.

***Pepsis gracilis* Lepell.**

One from Bartica, March 4, which I identify as this species not recognized in the Lucas monograph. It was described from Cayenne. A slender black species with reddish wings; quite hairy on head, front coxae and pleura; mesosternum with only short hair; the tubercle at base of coxal slope, tip rounded. Striae on propodeum fairly regular, no mid-ridge, lateral tubercles rather sharp and prominent; hind tibia above with small sloping teeth; not as far apart as in *ruficornis*, spines also sloping, little longer than teeth; third submarginal cell about as in the Lucas figure 131.

***Pepsis* sp. near *smaragdina*.**

One from Arakaka, December 21.

***Pepsis nireus* Moc.**

A male from Forest Settlement, Rio Mazaruni, August-September. Also recorded from Brazil.

***Pepsis festiva* Fabr.**

*Pepsis thalassina* Erichs., described from British Guiana, is a synonym, but no specimens in these collections. Also recorded from Surinam and Brazil.

**CRYPTOCHEILINAE.**

Table of genera.

1. Claws bifid, no lateral spines to last joint of mid- and hind tarsi; basal vein interstitial or only a little before transverse ..... 2  
Claws toothed ..... 3
2. Last joint of mid- and hind tarsi with a median row of spines; last segment of abdomen not compressed, antennae situate well above clypeus, distinctly slender toward tip; pronotum very short, hardly any dorsal part.....  
..... *Priochilus*  
No spines on last joint of mid- and hind tarsi; last segment of abdomen compressed; antennae close to clypeal margin, distinctly somewhat clavate; pronotum moderately long, the distinct dorsal part nearly or quite flat, the front part vertical or almost so.....  
..... *Balboana*
3. No lateral spines to last joint of mid- and hind tarsi; hind tibiae with more

or less distinct teeth above. *Priocnemis*  
Distinct lateral spines to last joint of mid- and hind tarsi..... 4

4. A stout slightly curved spine or tooth in front of each mid-coxa; venter of female (sometimes male) swollen, or with raised areas, or teat-like processes ..... *Priocnemioides*  
No such spine in front of mid-coxae; venter not modified; joints of flagellum moderately long; clypeus truncate ..... *Calopompilus*

***Priocnemis (Calicurgus) nubilus* Fox.**

Bartica, February 12, 24, May 26; Kartabo, July 19, December, 1920. *Priocnemis sericeicornatus* Cameron is, I believe, the same species.

***Calopompilus vitreus* Fox.**

Kartabo, October 30. Also recorded from Rio, Brazil.

It has a much shorter pronotum than the typical North American forms and is much less hairy.

***Priocnemioides* Radoszkowski.**

This was separated from *Priocnemis* because the third antennal joint was about as short as those beyond, and the hind tibiae were said to have two rows of strong spines above. He included two described species, *Pompilus fulvicornis* Cresson and *P. flam-mipennis* Smith, and described a new species which he supposed to be from Spain.

Later Schulz noted that these species had two raised, somewhat teat-like, areas on the ventral side of the second segment. The length of the third antennal joint is plainly longer in some forms, otherwise similar, and which have very distinct ventral teats. Moreover the second ventral varies in shape of the raised areas, sometimes a broad curved ridge, sometimes two flat areas; but in all these forms there is a distinct somewhat curved tooth or spine in front of each mid-coxa, this is not present in the genotype of *Cryptochilus*, nor in genotype of *Salius*, nor do these genera have the modified second ventral segment.

I select *Pompilus fulvicornis* Cresson as the genotype. There are many species in South America.

The five species I have seen from British Guiana are readily separable as follows:

1. Wings black or nearly so..... 2  
Wings yellowish ..... 3
2. Head and thorax with golden pile.....  
..... *aurifrons*  
Head and thorax without golden pile ..... *bituberculatus*
3. Head and thorax with much golden pubescence ..... *gigas*  
Head and thorax not golden, black.. 4



4. Body more or less purple, also much of the legs.....*purpureipes*  
 Body black, no purple, abdomen above somewhat punctate; vertex coarsely punctate ..... *perpunctatus*

***Priocnemioides gigas* Fabr.**

Kartabo, No. 20593; April 29, March 3, 5, Penal Settlement, Kartabo, July, No. 192. Bartica, February 11. *Priocnemis croesus* Smith is, I believe, a synonym. Also recorded from Brazil.

***Priocnemioides perpunctatus* Fox.**

Kartabo, April 14. Also recorded from Brazil.

***Priocnemioides purpureipes* Cam.**

Kalacoon, Georgetown, November 10; No. Hym. 251,280. Described from Demerara.

***Priocnemioides bituberculatus* Guer.**

A male from Kamakusa which I presume is the male of this species. It is not the male of *mammillatus*; in the latter species the subgenital plate is less broad than in this specimen. In both species this plate and the preceding segment are clothed with short, erect black hair; the ventral segments are punctate; in *mammillatus* the punctures are as dense in the middle of the segment as on sides, in this specimen there are few or none in the middle, but plenty on each side. In the hind wing the anal vein ends at forking of cubitus. The black on antennae extends only to tip of third joint; the body is black, without a blue tinge; the hair below the hind basitarsus is as short as in *mammillatus*. *Salus tuberculiventris* Cameron from Demerara is probably a synonym of *bituberculatus*.

***Priocnemioides aurifrons* sp. nov.**

Black, clypeus and face densely covered with golden pubescence, also, but scarcely as bright, on pleura, coxae, middle of mesonotum, scutellum, metanotum, and over entire propodeum, less distinctly on upper side of basal segment of abdomen. Wings dark brown, with a reddish iridescence, a little darker than in *tinctipennis*, tip narrowly pale; antennae black to end of fourth joint, upper side of fifth and partially on sixth, beyond rufous to yellowish, but last three joints brown.

Structure much like other species; clypeus rather deeply emarginate below; ocelli in low triangle, hind ocelli almost twice as near each other as to the eyes; vertex-width almost equal to third antennal joint, latter longer than fourth; propodeum coarsely ridged in posterior part, more coarsely than in *mammillatus* or *bituberculatus*; second ventral segment with a narrow raised area each side behind; subgenital plate about as broad as in *mammillatus*, with short dense

erect hair, and also on the preceding segment, but others with only scattered long hairs.

Front femora with some short, fine hairs above; hind tibia with rows of short spines much as other species, but those above very numerous and fine; inner spur of hind tibia about one-third of basitarsus, latter with a longer and denser fringe than in other dark-winged species.

Venation about as usual; the first recurrent vein, however, ends further from tip of second submarginal cell than usual, the second recurrent angulate near middle, ending much before middle of third submarginal cell, the latter much longer than the second; in hind wings the anal vein ends just beyond the forking of cubitus.

Length of fore wing 20 mm.

One male from Demerara River, March 20 (Cornell).

***Balboana fulvipes* sp. nov.**

Head, thorax, propodeum, and abdomen dull black; tip of abdomen and sides of first segment fulvous; antennae black, but basal joint fulvous below; legs fulvous, coxae also, tips of tarsal joints dark, spurs white; palpi pale. Fore wings hyaline, with two narrow black bands, one over basal and transverse veins, other occupying base of marginal, all of second and third submarginal, and upper part of third discoidal cells; hind wings hyaline. Clypeus about four times as broad as long, slightly convex below, surface with short hair; face scarcely narrowed above, ocelli in a broad triangle, lateral ocelli about as close to eyes as to each other; antennae plainly a little thickened toward tip; third joint not longer than fourth; pronotum arcuate behind; propodeum finely transversely rugulose, no median groove; abdomen rather slender, compressed at tip, last two segments hairy, venter with a few erect hairs. Head, thorax and abdomen mostly covered with very short, appressed white hair.

Legs smooth on femora and tibiae, hind tibia has about eight or ten short fine bristles above, one or two on the sides, inner spur nearly equal to one-half of the basitarsus.

Fore wings rather short, but slender, the marginal cell long, widest at end of second submarginal cell, from there sloping to acute tip, not one-half its length from wingtip; second submarginal cell about as high as long, both ends oblique, receiving the first recurrent at basal third; third submarginal fully three times its length from outer margin, a little longer than the second, narrowed about one-third above, outer side very oblique, receiving the second recurrent (strongly bent outward at middle) at about middle; lower basal vein slightly bowed for-

ward near end, meeting end of transversè, which is not oblique, in hind wings the anal ends much before forking of cubitus.

Length of fore wings 6 mm.

One from Kartabo, July-August.

Much smaller, and with less spiny legs and the dorsal part of pronotum longer than in typical *Balboana*, but agreeing in the clavate antennae, compressed tip of abdomen, antennae at clypeal margin and venation. There are several other species of this genus in South America.

***Balboana auripennis* Fabr.**

Kartabo, April 16, June 1, November 4, March 13, 17, September 26; Bartica, December 2. Also recorded from Brazil. The description of *Pompilus moorei* Cam. from Demerara fits *auripennis*.

***Priochilus*.**

This is agenoid in form, but larger and readily separated by the cleft claws and the median row of spines below on last joint of mid- and hind tarsi; in the smaller species these spines may be reduced to one or two. Moreover in the larger specimens there are one or two very small but distinct spine-pits on the hind femora toward tip. This with the tarsal armature would place the genus in the *Psammocharinae*, but there is no real "pocket" in the base of third discoidal cell. The hind tibiae have larger spines than in *Pseudagenia* and allies, mostly in one or two rows, in or near a carina. The venation is much like those *Pseudogenias* with a long third submarginal cell, but it is wider at tip; in hind wing the anal ends at or very near forking of cubitus; the basal segment of abdomen is not petiolate, and no distinct groove on the second ventral segment, but the segment is transversely impressed where the groove would be if present.

Type, *Pompilus nobilis* Fabr.

Includes at least fifteen or twenty neotropical species which were placed in *Agenia* or *Salix*.

**FEMALES.**

1. Fore wings black..... 2  
Fore wings pale, clouded or banded with dark..... 6
2. Face, thorax, propodeum and abdomen with much silvery, propodeum hairy behind..... 3  
Face silvery, little elsewhere..... 4
3. Mesosternum projecting laterally in an almost cone-like hump; carina of hind tibia slightly undulate, upper spines very short; mid-tibia enlarged and with many short spines, second submarginal cell much longer than high.....*superbus*

Mesosternum not projecting cone-like; carina of hind tibia not undulate, some upper spines nearly as long as width of joint, mid-tibiae slender, with fewer and longer spines; second submarginal cell only a little longer than high....

- .....*regius*
4. Second submarginal cell only a little if any longer than high, both ends oblique, propodeum hairy, face somewhat silvery.....*rhomboideus*  
Second submarginal cell plainly longer than high, ends less oblique..... 5
  5. Propodeum with long black hair above; clypeus very hairy all over, margin not polished; second submarginal cell almost twice as long as high, third submarginal very wide at tip; anal in hind wings ends beyond forking of cubitus.....*imperius*  
Propodeum with only very short fine hair, hardly noticeable; clypeus with only a few hairs in a row, margin polished, shining; second submarginal cell about one and one-half times as long as high, third submarginal cell not so wide at tip; anal in hind wings at forking of cubitus.....*plutonis*
  6. Abdomen yellowish-brown; propodeum not hairy above; outer dark band on fore wings very broad, inner band extended basally.....*formosus*  
Abdomen black..... 7
  7. Propodeum hairy above, narrowly silvery at base, broadly behind; wing hyaline between the bands, large species.....*nobilis*  
Propodeum not hairy, and little if any silvery, second submarginal cell often higher than long..... 8
  8. Propodeum transversely striate behind; front with somewhat golden pubescence.....*sericeifrons*  
Propodeum not striate..... 9
  9. No silvery nor golden at sides of scutellum; front opaque black, small species.....*opacifrons*  
A silvery spot at each side of scutellum..... 10
  10. Fore wings yellowish between the bands, no golden pubescence on front or notum.....*scrupulus*  
Fore wings hyaline between bands, some golden pubescence on front and notum.....*diversus*

***Priochilus regius* Fabr.**

Kartabo, March 4, April 28, August, Nos. 146, 218, 1929, 20213, 20462, 201297; Kamakusa, September, Forest Settlement, Rio Mazaruni August; Kalacoon; February 8, January 21, March 4; Penal Settlement, Oc-

tober 7; Demerara River, March 10, 18. Also recorded from Brazil.

***Priochilus rhomboideus* Fox.**

Bartica, March 5, May 8, 21, 24; Bartica, January 25; Arakaka, December 21; Turesi Falls, October 11; Mt. Everard, November 15; Georgetown, November 10, 15; Demerara River, March 8, 24. Also recorded from Brazil.

***Priochilus nobilis* Fabr.**

Kartabo, April 4; Bartica, February 18, April 15; Tropical Research Laboratory. Also recorded from Brazil. *Pompilus cosmopteryx* Cam. appears to be a synonym.

***Priochilus scrupulus* Fox.**

Kartabo, August, Nos. 20558, 21139. Also recorded from Brazil.

***Priochilus diversus* Sm.**

Kamakusa, September. Also recorded from Brazil.

***Priochilus sericeifrons* Fox.**

Bartica, January 28, February 4. *Pompilus harperi* Cam. appears to be this species; it is from Demerara. Also recorded from Brazil.

***Priochilus opacifrons* Fox.**

Bartica, January 29, February 5, March 5, April 3, 14, July, Hym. 306. December 23; Demerara River, March 19, 20, 26, 29, Mackenzie, Demerara River, June 23. Described from island of Jamaica, but these specimens appear to be the same and Fox records it from Brazil.

***Priochilus imperius* sp. nov.**

Black throughout, no silvery on face or on the coxae; wings with violaceous and bluish reflections. Face and vertex rather more hairy than other species; propodeum with long hair, abdomen above hairy near tip, venter hairy on last four joints. In general structure similar to other species; antennae very slender, third joint much longer than width of vertex; ocelli in a low triangle, laterals nearer each other than to eyes; pronotum broadly arcuate behind; metanotum finely striate; propodeum evenly convex, pleura hairy; legs slender, not hairy; hind tibia with carina above which is faintly cut into sections, hardly teeth, the bristles not one-half diameter of hind tibia; last joint of hind tarsus with a median row of four or five rather large spines below; long spur of hind tibia not one-third of basitarsus.

In fore wings the marginal cell is very long, hardly one-half its length from wing-tip; second submarginal cell longer than high, its basal side more oblique, receiving the first recurrent at about one-fourth from

tip; third submarginal cell one-half longer below than the second, very much widened at tip, narrowed one-third above, the outer vein almost angulate in middle; receiving the second recurrent (faintly sinuous) near end of basal third.

In hind wings the anal ends close to the cubital fork, and the cross-vein is beyond the middle of radial sector.

Length of fore wing 22 mm.

Females, one Kamakusa (Lang) (Bequaert coll.) and other Kartabo, June 24 (Beebe), both British Guiana. It will not fit *pilifrons* Cam. (which does not belong to this genus) nor *dives* Lepell. (which may be a *Priochilus*), and is not in the H. H. Smith collection of Carnegie Museum.

Others from Kamakusa; Moengo Boven Cottaca R., Surinam, May 14; Rio Itaya, Amazon, Peru, December; Guayaquil, Ecuador, May-June (Brues); Santa Cruz, Bolivia (Steinbach); La Sombra, Peru.

***Priochilus superbus* sp. nov.**

In general very similar to *P. regius*, usually larger. Clypeus and face one-half way up to ocelli silvery; collar and lower sides of pronotum, propodeum above, apical half of basal abdominal segment, basal third of second, coxae and apex of the mesopleura strongly silvery. A spot each side at base of third segment, and more or less on fourth and fifth segments less strongly silvery. Wings deep black.

Structure in general much like *P. regius*, ocelli in a broader triangle, third antennal joint proportionally not as long as in *regius*; propodeum slightly, evenly convex, hairy, especially behind; the mesosternum in front of mid-coxae projects outward in a prominent cone (only bulging slightly in *regius*); venter more hairy than in *regius*.

The mid-tibiae are slightly enlarged, and with more numerous and shorter spines than in *regius*. In the fore wings the second submarginal cell is plainly longer than high, longer than in *regius*, otherwise venation similar.

Length of fore wing 15 to 18 mm.

Holotype from Kamakusa, September. Paratypes from Villavicencio, Colombia; Chounazu, Peru, July 9; and several from Iquitos San Rogue, Peru, February, March, May; Santa Cruz, Bolivia.

The slightly enlarged, more spinose mid-tibiae, as well as the swollen mesosternum near mid-coxae, readily distinguish it.

***Priochilus plutonius* sp. nov.**

Black, no silvery, wings somewhat violaceous. Clypeus short, very broad, truncate below, the margin polished and shining, a row of long bristles across clypeus, otherwise without hair; face bare, front with two long erect hairs each side near orbits; ocelli

in a moderately narrow triangle, hind ocelli little more than diameter apart, much farther from the eyes; antennae slender, the third joint very long, longer than vertex-width; pronotum with only a few short, fine hairs, angularly emarginate behind; mesonotum with one or two erect hairs each side.

Propodeum without hair, opaque; tip of abdomen hairy on last few segments, above with some stiff bristles; legs long and slender, mid-tibiae with two rows of spines above, the longest about one-half the diameter of the joint, hind tibiae with a row of very short spines above, but no distinct carina, some spines on outer side one-half diameter of joint, long spur not one-third of basitarsus. In the fore wings the marginal cell is very long and slender, sharp pointed at each end, and less than one-half its length from wing-tip; second submarginal cell hardly one-half longer than high, each end oblique, receiving the first recurrent vein at about one-fourth from tip; third submarginal cell about as long above as second, much longer below, outer side sloping, receiving the second recurrent (almost bent in middle) at about basal fourth; lower part of basal vein straight, ending a little before transverse vein, latter not oblique; in hind wings the anal vein ends at the cubital forking.

Length of fore wing 13 mm.

A female from Demerara, British Guiana, March 10 (Cornell).

*Priochilus formosus* sp. nov.

Black; abdomen brownish-yellow or rusty brown; wings hyaline, a broad brown band out from basal vein and behind the cubitus extending back almost to base of wing; a still broader brown band over most of marginal cell, over both second and third submarginals, and most of the third discoidal cell; hind wings with the tip brown. Face and clypeus only faintly silvery, also faintly behind on propodeum, coxae more strongly silvery.

Clypeus shaped much like that of *regius*, broadly truncate below; face a little narrowed above, third antennal joint equal to vertex-width, and much longer than the fourth joint; median groove reaching anterior ocellus, hind ocelli hardly more than diameter apart, much farther from the eyes, a few long hairs in a row across clypeus, and two erect bristles each side by upper orbits, mesonotum and scutellum also with few hairs, more on the propodeum.

Pronotum broadly arcuate behind; propodeum with a rather broad median groove, from side propodeum shows an even slope, hardly convex.

Basal segment of abdomen from above with almost straight sides; tip of abdomen

above and below with fine hairs, some above are stiff.

Legs moderately slender; hind tibia with the longest spines about one-half diameter of the joint, inner spur not one-third of basitarsus.

Fore wings with marginal cell long, at widest no broader than second submarginal, nearly equally pointed at each end, hardly half its length from wing-tip; second submarginal one and one-half times as long as high, both ends oblique, receiving the first recurrent a little before tip, third submarginal scarcely longer than second above, but longer below, receiving the second recurrent (slightly sinuous) at before end of basal third; lower part of basal vein straight, ending scarcely before the transverse, which is hardly oblique; in hind wing the anal vein ends much before the forking of cubitus.

Length of fore wing 13 to 15 mm.

Holotype from Kamakusa, British Guiana, paratype from El Campanentus, Col. Parene, Peru, July 1 (Cornell). It differs in many points from *abdominalis* Sm.

PSEUDAGENINAE.

Table of genera.

1. Mid- and hind tarsi with bristles and spines on lateral edges of last joint; hind tibia with only small spines above, and indistinct carina.....*Phanochilus*  
Mid- and hind tarsi without spines under last joint or not laterally..... 2
2. Hind tibia with teeth above (sometimes very small); antennae situate hardly diameter of basal joint above clypeus ..... 5  
Hind tibia without teeth..... 3
3. Propodeum without hair; rarely a distinct "beard," sometimes a few short hairs; claws toothed.....*Agieniella*  
Propodeum more or less hairy; usually a distinct "beard," several long stout bristles ..... 4
4. Usually a carina above on hind tibia, and one or more rows of short spines; antennae situate rather high above clypeus; anal vein of hind wings ends beyond or at forking of cubitus.....  
.....*Priocnemella*  
No carina, few spines on hind tibia; in hind wings anal vein ends before the forking of cubitus .....*Pseudagenia*
5. A distinct "beard" under the head  
.....*Alasagenia*  
No "beard" under head.....*Priophanes*

*Alasagenia* gen. nov.

Abdomen with distinct petiole; venation as in *Pseudagenia*; a beard of six or more

rather long hairs under head; in a transverse row last joint of mid- and hind tarsi bare beneath; claws toothed; basal vein ends before the transverse; in hind wings anal vein ends before forking of cubitus; hind tibia with a row of distinct teeth above, and on each side a row of short bristles.

Type *A. erichsoni* sp. nov.

Some species from the United States have been put in *Priocnemis*, but differ in the petiolate abdomen.

***Alasagenia erichsoni* sp. nov.**

Body, antennae and legs deep black, clypeus and sides of face strongly silvery, a silvery spot each side on hind border of pronotum, also the hind border of mesonotum, sides of metanotum, a large square silvery spot each side on posterior slope of propodeum and the base also silvery; also silvery spots on the pleura, front coxae, part of basal abdominal segment, a large spot each side on second segment, basal half of third, and less distinctly across fourth and fifth.

Fore wings hyaline, a narrow dark band over basal and transverse veins, a broader band beyond stigma, but not quite reaching across third discoidal cell, tip plainly brownish; in hind wing the tip is smoky. Head, thorax, propodeum with much fine pale hair, and some longer, erect ones.

Clypeus nearly three times as broad as long, lower margin evenly, but slightly, concave, rather closely parallel to upper edge; face only a little narrowed above, vertex-width hardly as long as second plus third antennal joints; hind ocelli about equally near each other and to eyes; pronotum slightly angulate behind; propodeum rather low, evenly convex, no distinct dorsal groove; basal abdominal segment with a little short hair on petiole above, some fine hair on last few segments, and a few on venter.

Legs with femora moderately stout, hind tibia above with a row of distinct teeth and an inner carina, the spines extremely short; inner spur of hind tibia not two-fifths of basitarsus.

In fore wings the marginal cell is long, not as broad as the second submarginal, less than two-thirds of its length from wing-tip; second submarginal cell but little longer than high, not longer above, receiving the first recurrent vein at apical third; third submarginal about twice as long as second, the outer side oblique and rather strongly curved on lower third, receiving the second recurrent (much bent near middle) at middle of cell, the cell about two-thirds its length from outer margin; basal vein ends much before the transverse, latter a little oblique; in hind wing the anal vein ends at forking of cubitus.

Length of fore wing 10 mm.

From Kartabo, February 28. Named for W. F. Erichson, who described many insects from British Guiana.

***Priophanes fabricii* sp. nov.**

Head black, clypeus yellow, face with short white pile, most noticeable at orbits; thorax and propodeum rufous; abdomen shining black, second, third, and fourth segments with a large spot of silvery pubescence each side; antennae black; legs yellowish, femora somewhat brown above, hind tibiae rather darker, coxae and trochanters black. Fore wings hyaline, stigma brown, a narrow brown band over basal and transverse veins, a broader brown band beyond stigma, but not extending behind third discoidal cell, tip of wing slightly brown. Hind wings not marked. Clypeus about three times as long as broad almost pointed at each end, upper and lower edges nearly equally evenly convex; palpi especially third joint, very long. Face broadest in middle, more narrowed above than below, vertex-width longer than second plus third antennal joints; hind ocelli almost as near eyes as to each other; pronotum slightly angulate behind; propodeum evenly convexly sloping, posterior half with some long pale hairs, no median groove.

First segment of abdomen with pendent sides, tip with very fine hair, on venter a few short hairs; legs with femora very smooth, the hind tibiae with very minute, hardly visible teeth, the spines very short, black, three rows of them above, mid-tibia similar, inner spur of hind tibia fully two-fifths, but not one-half, of basitarsus.

In the fore wings the marginal cell is moderately long, about two-thirds its length from wing-tip, equally broad at ends of second and third submarginal cells; second submarginal cell nearly one and a half times as long as broad, both ends oblique, receiving the first recurrent vein before middle; the third submarginal about one-half its length from outer margin, above fully as long as the second submarginal, below one-third longer, outer end not strongly oblique, receiving the second recurrent (scarcely curved) before end of basal third; basal vein ends much before the transverse; in hind wing the anal vein ends before forking of cubitus.

Length of fore wing 6 mm.

Type from Kartabo, July-August. Two paratypes, one St. Augustine, Trinidad, March 23, other Restrepo, Dept. Meta, Colombia. The one from Trinidad has the hind ocelli a little nearer to each other than in type, and the Colombian specimen has the hind ocelli a little nearer eyes than in type. Named for J. C. Fabricius, who first described various species from this region.

**Phanochilus** gen. nov.

These have the general appearance of a large *Pseudagenia* or *Priochilus*, the basal abdominal segment being plainly petiolate and the venation is much like them; the basal vein is more separated than usual in *Pseudagenia*. In the hind wing the anal vein ends near or at forking of cubitus. The hind tibia may be toothed, or with a low carina which is broken by a row of very short spines; the last joint of mid- and hind tarsi have a few spines or bristles near each margin; the claws are toothed; the clypeus is often somewhat hexagonal; the head seen from above is rather quadrate, being much more swollen behind than usual; the mesopleura projects laterally, into a large cone-like swelling, readily seen from above.

Type *Agenia nobilitata* Smith.

**Phanochilus nobilitata** Sm.

Tropical Research Station No. 21265. Have also seen it from Rio Itaya, Amazonas, Peru.

The *Salix fuscomarginatus* Fox is very similar, but a heavier insect and the malar space is much broader.

**Phanochilus gloriosa** Sm.

One male from Kartabo, July 16. Also recorded from Brazil. *Salix aureodecoratus* Cam. described from Demerara, appears to be this species. I see no difference between this species and the male of *nobilitata* except the dark cloud in wing of *gloriosa*.

**Phanochilus pilifrons** Cam.

Described from Demerara; specimens examined are from Kamakusa, September, Bartica, January 31, and Rio Essequibo (J. Ogilvie).

**AGENIELLA.**

## Females.

1. Body wholly yellowish; wings hyaline, with a large black spot at tip...*reversa*  
Body not wholly yellowish, wings with two dark bands..... 2
2. Thorax reddish, legs black, apical part of antennae pale.....*micans*  
Thorax, black, antennae partly yellowish.....*delila*

**Ageniella micans** Fabr.

Tumatumari, Potaro River, June 28, one male. The *Pseudagenia pulchricornis* Cam. described from Demerara is this species; I have also seen it from the Matto Grosso of Brazil.

**Ageniella reversa** Sm.

Tumatumari, Potaro River, June 29. Also recorded from Brazil.

**Ageniella delila** sp. nov.

Body, thorax, legs, abdomen dull black; antennae with basal joint pale beneath, beyond black to middle of sixth joint, thence yellowish; a small silvery to golden spot each side at end of propodeum. Wings hyaline, fore wings with a moderately broad straight brown band across over basal and transverse veins; another brown band over basal part of marginal, most of second submarginal, basal part of third submarginal, and apical part of third discoidal cells, no broader than the other band, tip of wings scarcely fumose; hind wings unmarked.

Clypeus about three times as broad as long, lower margin evenly rounded; ocelli in a small triangle, laterals much nearer to each other than to eyes; pronotum scarcely angulate behind; propodeum low, no median groove; abdomen petiolate, basal segment very slender just before attachment. No hairs on body except at tip of abdomen. Legs slender, smooth, mid- and hind tibiae with only extremely minute bristles above, inner spur of hind tibia about two-fifths of basitarsus.

Fore wings with marginal cell broad at end of second submarginal cell, fully twice as broad as the second submarginal, about two-thirds of its length from the wing-tip; second submarginal cell very small, slightly broader at base which is about two-thirds of its length, receiving the first recurrent vein at middle; third submarginal cell longer above than second below, and below twice as long as second, less than its length from outer margin, receiving the second recurrent (bent below middle) before end of basal third; basal vein ends a short distance before transverse; in hind wing the anal vein ends much before forking of cubitus.

Length fore wing 7.6 mm.

From Kartabo, July-August.

The male has a more slender body; is similar in color except that the antennae is yellowish, with the fifth, sixth, and seventh joints dark.

The clypeus is very broadly and deeply excavate on the lower margin and each end projects as a tooth; its surface has much short hair. The structure is also very similar to the female, but the basal abdominal segment is more slender, and with pendent sides; the mid- and hind tibiae have very minute spines on sides and above, the inner spur of hind tibia is a little longer, but does not reach middle of basitarsus; there are no hairs at tip of abdomen. The venation is also similar, but the marginal cell is not quite so broad, and the second submarginal broader, but no longer than in female.

Length 7 to 8 mm.



From Demerara River, March 10, 12, 18 (Cornell).

**PSEUDAGENIA.**

Females.

1. Mid- and hind femora black, mid-tibiae rufous; clypeus hardly rufous below; pygidium black.....*incrota*  
At least hind femora reddish..... 2
2. Only hind femora reddish, thorax black.....*comparata*  
Other femora at least partly reddish or yellowish..... 3
3. Thorax plainly bluish or greenish, metallic..... 4  
Thorax black above, dull; mid- and hind tibiae black or dark; pygidium black.....*smithi*
4. Mid- or hind tibiae more or less pale, thorax somewhat greenish; propodeum rather coarsely granulate, and on middle of basal part plainly transversely striate; pygidium dark.....*tarsata*  
Mid- and hind tibiae dark; propodeum only finely granulate, punctate behind, not striate above..... 5
5. Basal joint of antennae pale below; third antennal joint rather short, body rather slender; pygidium pale.....sp.  
Basal joint of antennae black below.....6
6. Thorax and propodeum more greenish; front and mid femora with much dark above especially toward base, pygidium brownish; propodeum with shorter hair, body rather slender.....sp.  
Thorax plainly bluish, femora wholly rufous, pygidium pale, propodeum with long white hair, body broader.....*femorata*

Two species I have not been able to identify, nor can I be sure they are new.

***Pseudagenia femorata* Fabr.**

From Demerara River, March 12, 22; Kartabo, March 10; No. 1925, May 7, No. 1925; Bartica, January 29, February 1. Also recorded from Brazil.

The basal vein ends plainly before transverse, latter scarcely oblique; third submarginal cell wider at tip than in *tarsata*; propodeum not coarsely granulate as in *tarsata*.

***Pseudagenia smithi* D. T.**

*Pseudagenia semisuaavis* Cam. from Demerara, is probably a synonym of this species. I have none from British Guiana but from northeastern Colombia, and it is recorded from Brazil. Basal vein nearly interstitial with transverse, latter oblique.

***Pseudagenia tarsata* Sm.**

From Kartabo June 9, August 17.

Basal vein ends only a trifle before the transverse, latter very oblique.

***Pseudagenia modesta* Sm.**

Male from Bartica, February 10. Also recorded from Para, Brazil.

***Pseudagenia comparata* Sm.**

From Kartabo, Tumatumari, March 10, Nos. 20419; 1925; June 28. Also recorded from Para, Brazil.

***Pseudagenia basalis* Sm.**

Male from Bartica, February 26. Also recorded from Santarem, Brazil.

***Pseudagenia incrota* sp. nov.**

Black, clypeus and lower face with silvery pubescence, antennae dull yellowish, last few joints brown, basal and ringjoint nearly black; lower parts of pronotum silvery, and a silvery spot each side behind, four silvery patches on propodeum, the two at hind border the larger; abdomen with some fine whitish hairs near tip; wings hyaline, stigma black, venation brownish, tip of fore wing faintly brown; legs brown to nearly black, the front pair rufous to yellowish beyond femora, the mid-tibiae rufous, tarsi dull black, hind legs wholly dull black.

Clypeus rather short, broadly rounded below; antennae rather slender, second plus third joints not equal to vertex width, hind ocelli nearer to each other than to eyes; pronotum broadly concave behind; propodeum evenly convex, median line very faint, mesosternum laterally bulging, but not sharply so; abdomen with fine bristles near tip; hind tibiae with a few minute bristles above, a median and shorter lateral rows, long spur about one-half of basitarsus.

In fore wings the marginal cell is much less than its length from the wing-tip, second submarginal cell not twice as long as high, receiving the first recurrent vein a little beyond the middle, third submarginal about one-half longer than second, and much wider at tip, receiving the second recurrent a little before middle, basal vein ends plainly before the transverse; in hind wings the anal vein ends much before cubital fork.

Length of fore wing 6 mm.

Females from Kamakusa (Lang, Bequaert), and Bartica, January 17, 1913 (Cornell), both British Guiana.

***Priocnemella eurytheme* sp. nov.**

In general coloration, the short fourth antennal joint, the short inner spur of hind tibia, the shape of clypeus, and golden pubescence this species is close to *Salix hexagonus* Fox. The golden pubescence, however, is more extensive; it is on face, the clypeus when viewed from above, golden band on hind margin of pronotum,

golden on mesonotum, middle spot on metanotum just behind the scutellum, also basal band and two large apical spots on the propodeum. A spot on pleura is golden to silvery, and there is a silvery sheen on sternum and coxae.

The lower margin of clypeus is about equally three-sided, the middle portion truncate; fourth joint of antennae much shorter than the third, and shorter than the joints beyond; face moderately narrow, orbits nearly parallel, hind ocelli much closer to each other than to eyes; pronotum arcuate behind; scutellum convex; propodeum about as broad as long, somewhat narrowed behind, no median furrow, from side evenly convex, at the turn are a few rather large transverse ridges, from side some very fine and very short hairs are scarcely noticeable.

Abdomen steel blue, metallic, some long hairs toward tip, venter with much long hair, and patches of dense and very short hair; legs black, front tarsi faintly brownish; hind tibiae with a row of very short bristles arising from a very low carina, but no distinct teeth; long spur of hind tibiae little more than a fourth of the basitarsus.

Fore wings with marginal cell long and sharp-pointed, widest at end of second submarginal cell, latter a little narrowed towards tip, base oblique, almost one and one-half times as long as broad, receiving the first recurrent a little before tip; third submarginal about twice as long and much wider at tip, narrowed one-third above, receiving the second recurrent vein (slightly curved) at about middle.

Length of fore wing 15 to 17 mm.

Two females, one from British Guiana, other Tropical Research Station at Kartabo, No. 117.

Related to *hexagonus* Fox which probably belongs to this genus.

*Priocnemella difformis* sp. nov.

Black throughout; head and thorax with bluish iridescence; wings somewhat violaceous; abdomen shining blue-black; clothed heavily with moderately long black hair on head above and below, pronotum, propodeum, pleura, all coxae, and venter of abdomen, a few on basal part of first segment above, on last segment with some long hairs, and with short hair above.

Clypeus punctate, lower edge slightly convex, not three times as broad as long; face slightly narrowed above, antennae slender, second and third joints together equal to vertex-width, ocelli in a low triangle, hind ones very much nearer each other than to eyes, the beard is a small group of slightly upcurved bristles; pronotum short, slightly angulate behind; metanotum elevated in middle and with erect

hairs, a few on hind part of scutellum, sides of metanotum not striate; propodeum rather low and evenly curved, from above as broad as long, with faint median groove.

Basal segment of abdomen rather long, petiolate, the petiole with concave sides. Legs slender, hind tibiae almost without spines, above, only a few extremely minute ones nearer outer side, a low carina near inner edge, inner spur hardly more than one-fourth of the basitarsus; mid-tibiae with some stouter, more distinct spines.

Fore wing with the marginal cell long, about two-thirds its length from wing-tip, hardly broader than the second submarginal cell, latter one and one-half times as long as broad, base curved, oblique, receiving the first recurrent vein near apical third; third submarginal almost twice as long as second below, at widest about twice as broad as second, narrowed one-third above, the outer side strongly oblique and faintly sinuous, its tip about one-third its length from outer border, receiving the second recurrent (slightly curved) at middle; basal vein but little oblique, ending much before the transverse; in hind wing the anal vein ends at or just beyond forking of cubitus.

Length of fore wing 16 mm.

Holotype from Kamakusa, paratypes from Iquitos San Rouge, Peru, April; and Buenavista, Santa Cruz, Bolivia. In appearance much like *Phanochilus pilifrons* Cam. and *Priochilus imperius* but differing very much in characters of mid- and hind tibiae and last tarsal joint. It is larger than indicated by Fabricius for *captivus*, and he does not mention bluish body nor violaceous wings.

PSAMMOCHARINAE.

The genera can be tabulated as follows:

1. With a line or sigma on middle of posterior part of pronotum..... 2  
No such sigma..... 3
2. Posterior part of propodeum humped each side.....*Arachnophroctonus*  
Posterior part of propodeum evenly rounded .....*Batazonus*
3. Pronotum elongate, front femora thickened, abdomen compressed, but two submarginal cells, no spines under last joint of mid- and hind tarsi.....*Planiceps*  
Pronotum not elongate..... 4
4. Clypeus emarginate in middle..... 5  
Clypeus not emarginate..... 6
5. Fore wings folding lengthwise; no spines under last joint of mid- and hind tarsi; thorax without hair.....*Aplochares*  
Fore wings not folding lengthwise; spines under last joint of mid- and hind tarsi .....*Notiochares*



6. No spines under last joint of mid- and hind tarsi; tip of abdomen with a few fine hairs; female with a tarsal comb; male with claws cleft.....*Seritopompilus*  
 Spines under last joint of mid- and hind tarsi; tip of abdomen with some stiff bristles ..... 7
7. Propodeum bare; marginal cell short .....*Pompilinus*  
 Propodeum hairy..... 8
8. Female with a tarsal comb.....*Psammochares*  
 Female without tarsal comb.....*Anoplius*

***Batazonus decedens* Sm.**

From Kartabo, No. 2121, February 26, March 4, June 3. Also recorded from Santarem and Para, Brazil.

***Batazonus fervidus* Sm.**

Kartabo, March 24, June 30, No. 24688; Bartica, February 4. Also recorded from Brazil.

***Batazonus polistoides* Sm.**

Kartabo, Nos. 1920(2); 282, 20945, May 14, 29; Rio Mazaruni, Forest Settlement, September, Demerara River, February 18, March 8, 19; Bartica, January 16, 27, February 12. Also recorded from Brazil.

***Arachnophroctonus crassidentatus* Cam.**

Described from Demerara. One from Kartabo, June 11, appears to be the same as *A. vulpes* Fox.

***Psammochares inculcatix* Cam.**

Described from Demerara; specimen before me from Surinam; it is close to and perhaps identical with more southern *P. triquetrus* Fox.

***Psammochares echinatus* Fox.**

Kartabo, No. 22136; July 23, October 10, May 18, March 27; Bartica, January 29, April 14; West Bank Demerara River, February 9. Also recorded from Brazil. The male is structurally very close to *P. ornamentus*, and with the fore wings entirely black.

***Psammochares ornamentus* Fox.**

Bartica, February 11, 24, 26, January 28; Kartabo, May 27, July-August; Essequibo River, June 26. Also recorded from Brazil. The size of the pale area in middle of wing varies, and so might be a variety of *echinatus*; there are slight differences in venation which I doubt will be constant; all specimens are males.

***Notiochares amethystina* Fabr.**

Kartabo, August 5, 1920 (2 spp); July 29, 1920; September 1, 1922; April 28,

1919; Penal Settlement, Nos. 320, 329; Tropical Research Station, Nos. 2045, 2048, 20306, 20307, 21105; Bartica, May 21, 1924.

This species is widely distributed from Paraguay to Colombia, and there are numerous specimens in the collection from British Guiana. Cameron's record of *imperialis* doubtless refers to this common species. In the forked subgenital plate and the short band of velvety hair it is extremely similar to *N. philadelphica* of the United States. A variety, less blue and covered with sericeous pile especially prominent on the propodeum, from Arakaka, does not differ from the typical in other characters.

***Aplochares* gen. nov.**

Clypeus elevated, convex, lower margin with a deep rounded emargination in middle; female with a comb, spines slender; mid- and hind tibia with slender spines; claws toothed; last joint of tarsus below with a few teeth in middle; wings tend to fold lengthwise as in *Episyrion*; marginal cell not its length from tip of wing, basal vein interstitial with the transverse, thorax, pleura and propodeum without hair; head bare, except two or three erect hairs each side on vertex; abdomen with fine hairs at tip; antennae slender. Type *Pompilus imitator* Smith. Differs from *Lophopompilus* and *Notiochares* (which also have emarginate clypeus) by absence of stiff bristles at tip of abdomen, the folding wings and absence of hair on much of body.

***Aplochares imitator* Sm.**

One from Kartabo, October 11. Also recorded from Brazil.

***Sericopompilus exilis* sp. nov.**

Male. Black with much sericeous pubescence especially on face, clypeus, pronotum and propodeum; pronotum with white band behind; abdomen with whitish spot each side on base of second and third segments, and last dorsal segment also white; legs mostly black; front tarsi paler, hind tibia with a whitish streak on basal half above, mid- and hind spurs white, front ones more rufous.

Wings hyaline, fore wings with dark band over basal and transverse veins, and a broader one occupying all but the base of marginal cell, apical half of second submarginal, apical part of third discoidal, and extending to tip of wing, where, however, it is much less dark than the beginning; hind wing with extreme tip dark; antennae often somewhat rufous toward base.

Lateral ocelli about as close to eyes as to each other; antennae thick, short; not reaching tip of scutellum; hardly any erect hairs on head, thorax, or propodeum, only the ap-

pressed pubescence; propodeum with median furrow; abdomen compressed particularly toward tip, no long hairs at tip; mid- and hind tibiae with a few moderately long spines above, and between the two main rows there is a more or less complete row (sometimes but two or three) of very much smaller spines, inner spur of hind tibia three-fourths as long as basitarsus, claws cleft.

In fore wing the marginal cell is pointed, and hardly its length from wing-tip; but two submarginals, no trace of third, the second fully half the length of the marginal cell below, but narrowed each end above, receiving the first recurrent plainly before middle, and the second recurrent (straight) a little before tip; basal vein interstitial or nearly so with the transverse. In hind wing the anal vein ends much before forking of cubitus.

Length of fore wing 6.5 to 7 mm.

Type from Bartica, British Guiana, March 20 (Cornell); paratype, Zanderij, Para district, Surinam, April 27.

*Planiceps pertyi* sp. nov.

Black; head and thorax with fine short pale pile which on hind part of pronotum, posterior part of mesonotum, and a broad streak each side on propodeum is yellowish, in some views almost golden. The second, third and fourth segments of abdomen have a pale yellowish spot each side, and the last segment has a median streak, almost white. The fore wings are yellowish, the hind pair less distinctly so; veins, except costal, mostly pale; in fore wings is a brown mark over basal vein, extending almost half way out in the second discoidal cell; another broader brown band occupies all but base of marginal cell, half of second submarginal and a like distance beyond, the two bands separated by more than the width of the outer band; tips of both wings faintly brown.

Clypeus proportionally a little longer than in *herberti*; front ocellus in a deep pit; hind ocelli about as near eyes as to each other; vertex fully as broad as the third plus fourth joints of the antennae; pronotum long, sides rounded, with distinct scattered punctures above; propodeum more slender than in *herberti*; abdomen very slender, with a few very fine hairs toward tip, and some along venter, mostly toward tip, front femora very broad.

Venation of fore wings much as in *herberti*, but the basal vein rather more bulging basally; hind wings also similar.

Length of fore wing 10 mm.

From Kartabo, April 13. Paratypes from Demerara River, March 24 (Cornell) and Tropical Research Station, No. 20655. (Beebe.)

*Anoplius varius* Fabr.

One male from Kartabo. Also recorded from Brazil.

The abdomen differs from that of *P. echinatus* and *P. ornamentus* in lacking the pale band on fourth segment as noted by Fabricius. The fore wings are dark only at tip; the male has a hair brush on the fourth ventral segment.

*Pompilinus orthodes* sp. nov.

Head, thorax, legs, antennae black, wings dark fuscous, abdomen with first three segments rufous, others black, extreme base of first segment black. Clypeus, and lower face silvery, coxae also somewhat silvery; few short hairs on vertex and pronotum, a row of longer hairs on clypeus, tip of abdomen above with stiff black bristles, venter with a few hairs.

Clypeus about three times as broad as long, lower edge truncate; face rather long and narrow; vertex-width hardly equal to second plus third antennal joints; pronotum an even curve to front, behind angulate in middle; propodeum a trifle longer than broad, from side an even curve, no hair.

Abdomen rather long, tip not compressed; legs smooth, a few very short, stiff bristles above on front femora, spines on basitarsus very short; mid-tibia with two rows of spines, outer row very stout; hind tibia with two rows of spines, inner row the longer, inner spur equal to half of basitarsus; claws toothed. In fore wings the marginal cell triangular, more than its length from wing-tip, second submarginal cell as broad as long below, shorter above, receiving the first recurrent vein at apical third; third submarginal cell nearly as long below as second, almost to a point above, fully twice its length from margin of wing, receiving the second recurrent (almost straight) at middle; basal vein interstitial with transverse; in hind wing the anal vein ends at forking of the cubitus.

Length fore wing 8.5 to 10 mm.

Two females, Georgetown, September 29 (Bequaert), and Kartabo, July-August (Wheeler).

NOTOCYPHINAE.

*Notocyphus vindex* Lucas.

One from Kaieteur, August 11. Also recorded from Brazil.

*Notocyphus tyrannicus* Lucas.

Recorded by Williams from British Guiana (Studies in Tropical Wasps, 1926, p. 133). Also recorded from Brazil.

Besides the above, Cameron describes two species from Demerara which I have not recognized in any material available to me, *Prionemis curtispinus*, *Pompilus demeraraensis*.

## 11.

Larval Crabs from Bermuda.<sup>1</sup>

MARIE V. LEBOUR.

*Naturalist at the Plymouth Laboratory.*

(Text-figures 1-19).

A certain number of crabs in berry were collected on the shore and their young hatched out in the laboratory of the Bermuda Biological Station. Also a few were taken in dredgings and hatched out and some megalopae were reared to young crabs. The larvae were not reared through series of stages or to the megalopae. It is however useful to describe these larvae, hitherto unknown, some of which show interesting features. A colored drawing was made from each zoea hatched from the egg and color notes are given here. A few breeding records were also noted.

## PORTUNIDAE.

The zoea was hatched out from the eggs of *Portunus sayi* and *P. depressifrons*. The megalopa of *Portunus anceps* was obtained from the plankton and reared to the young crab.

Both zoeae are typical portunids and so also was the megalopa.

*Portunus sayi* (Gibbes).

(Text-fig. 1).

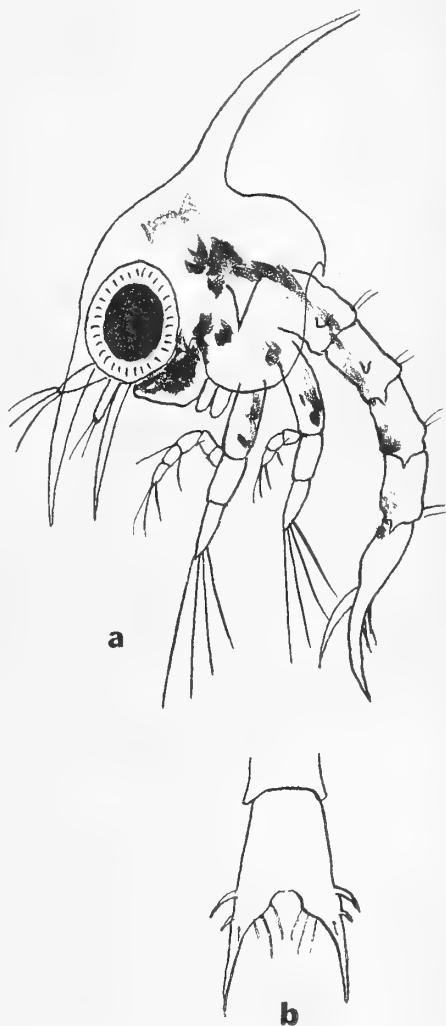
This species lives among floating *Sargassum* weed and is commonly found in the open water around Bermuda, sometimes drifting into the sheltered shallow bays in the Reach. It was found in berry from July to September. The eggs were 0.32 mm. across when nearly ready to hatch and were hatched July 1, 1938. The first zoea measured 1.2 mm. in length (from the front of the head region to the tips of the telson fork.) The body has a faint purplish-pink tinge and there are black chromatophores in the mouth region, in the thorax and abdomen and on the maxillipedes.

*Portunus depressifrons* (Stimpson).

(Text-fig. 2).

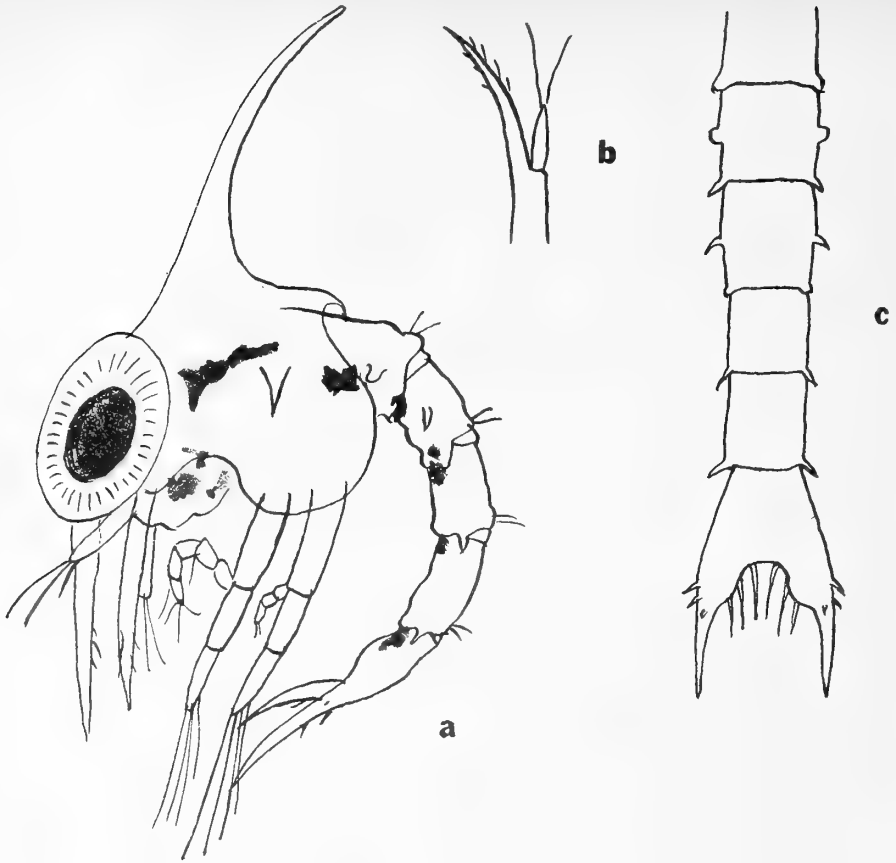
This species is very commonly dredged from sand in shallow water in the Reach, or obtained by pushing a hand net. In

dredgings taken in July and August, 1938, it was not breeding but in April, 1939, several were in berry and the zoeae were



TEXT-FIG. 1. *Portunus sayi*. **a.** Side view of first zoea, 1.2 mm. long. **b.** Telson.

<sup>1</sup> Contribution, Bermuda Biological Station for Research, Inc.



TEXT-FIG. 2. *Portunus depressifrons*. **a.** Side view of first zoea, 1.6 mm. long. **b.** Antenna. **c.** Abdomen and telson.

hatched on April 23. The eggs measured 0.36 mm. across when ready to hatch. They have a pinkish color in the early stages and are dark brown later. The first zoea measures 1.6 mm. in length. The lateral spines on the telson are very small, especially the posterior spine. The body is very transparent and colorless with concentrated black chromatophores in the mandibular region, in the center of the thorax and on the abdominal somites.

***Portunus anceps* (Saussure).**  
(Text-fig. 3).

This species is not common, but a megalopa was taken in the plankton from a night haul in the Reach, June 18, 1938, which changed to a crab. This and other species were kindly named by Professor Garstang.

The megalopa was large, the cast skin measuring 7 mm. long from the tip of the rostrum to the end of the telson. When living it was pale greenish-yellow with a very few dark chromatophores. The uropods bear 16 setae. The rostrum is long and straight.

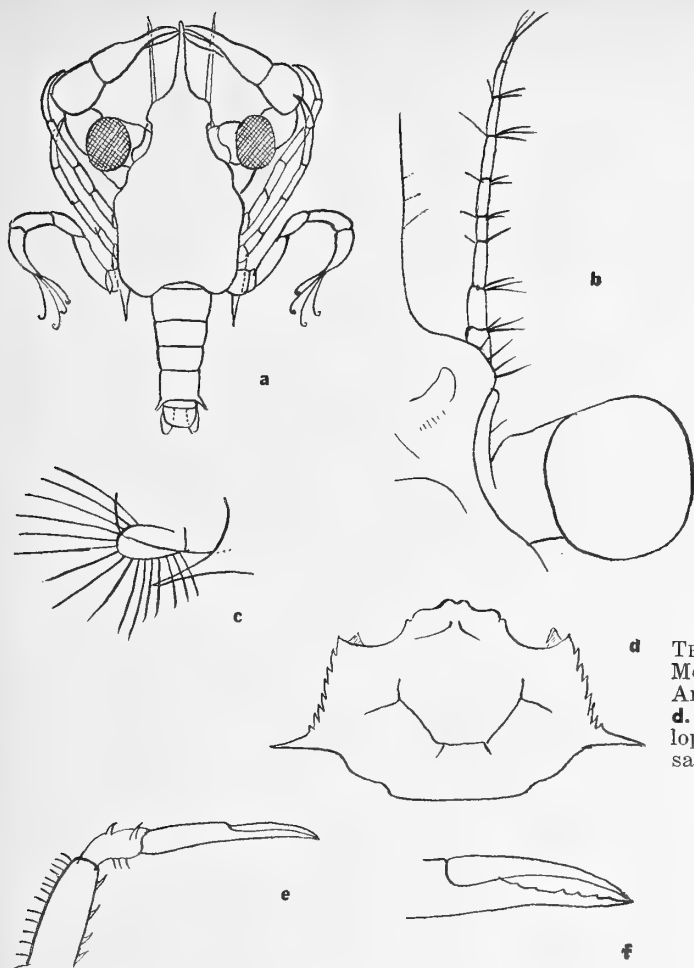
The first crab stage from the megalopa was pale yellowish with very powerful paddles. Unfortunately it died in casting its skin to the second crab stage. The carapace measured 6 mm. across with a very long lateral spine and 8 teeth in front of it.

**GRAPSIDAE.**

The zoeae of *Planes minutus*, *Pachygrapsus transversus* and *Percnon gibbesii* were hatched from the egg. *Planes* and *Pachygrapsus* are typical grapsids, but *Percnon*, belonging to the Plagusinae, has some interesting and peculiar features.

***Planes minutus* (L.).**  
(Text-fig. 4).

The zoea of this little Sargassum Crab has been described by Hyman (1924), who hatched it from the egg. It is extremely common in the *Sargassum* weed all round Bermuda and was breeding freely from June to October and from March to June, occasionally in other months, so that there is hardly a month in which it cannot be



TEXT-FIG. 3. *Portunus anceps*. **a.** Megalopa, cast skin, 7 mm. long. **b.** Anterior end. **c.** Telson and uropod. **d.** Carapace of first crab from megalopa. **e.** End of first leg. **f.** Chela of same.

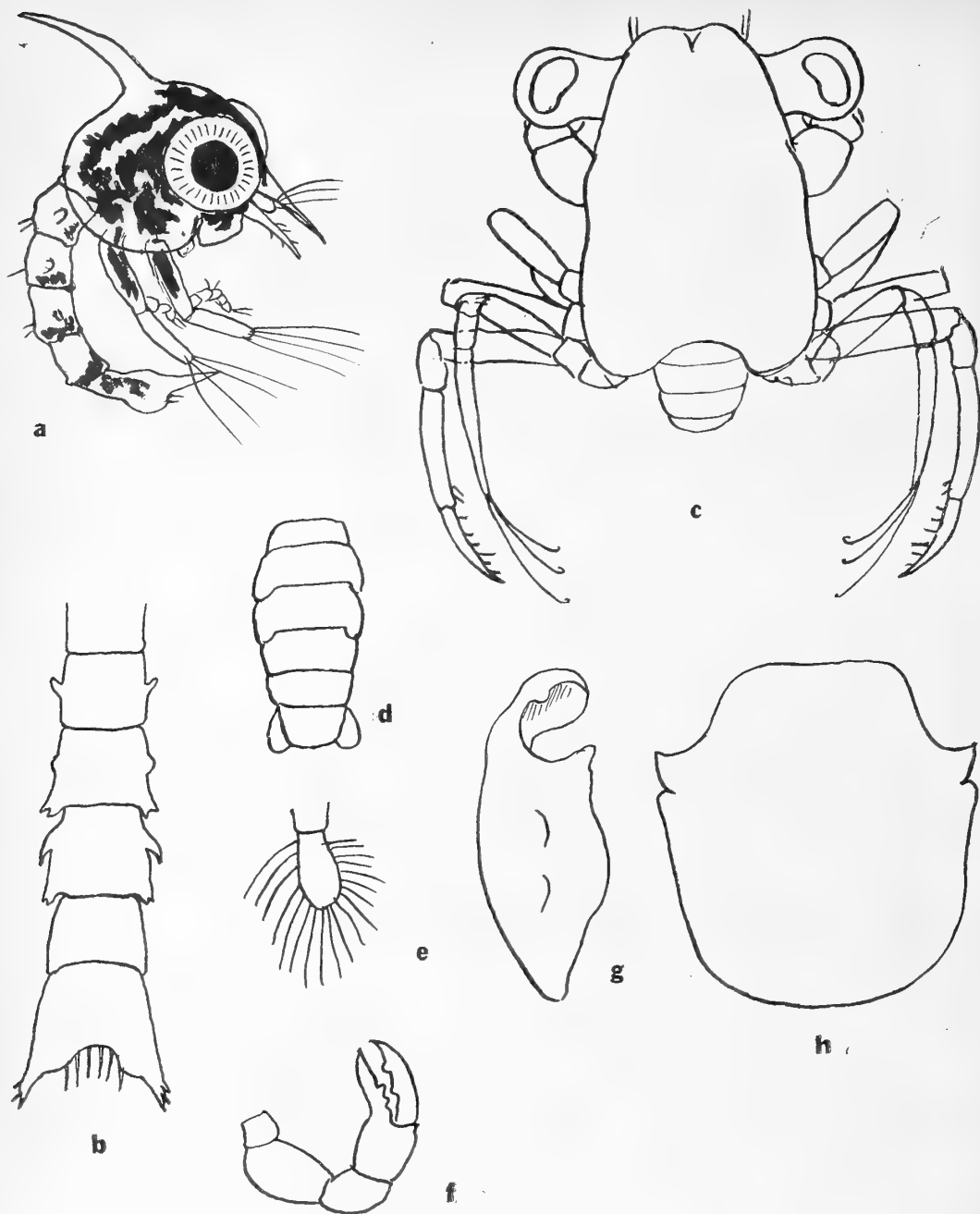
found in berry. The eggs were hatched out on June 13, 1938, and several times afterwards. They are dark brown in the mass, and measure 0.36 mm. across when nearly ready to hatch. The first zoea, 1 mm. in length, has much black pigment thickly spread on the thorax and in patches on the abdomen, the whole body being a very pale yellow so that the appearance is greenish. There are no lateral spines on the carapace and the dorsal spine is slightly longer than the rostral, both being short. There are forwardly directed knobs on the second abdominal somite, outwardly directed knobs on the third and backwardly directed knobs on the fourth. The third and fourth somite end postero-laterally in a process with 2 teeth. This is slightly different from Hyman's description and figure. The telson ends in a fork only slightly widened posteriorly with 3 teeth externally at the end of the forks and 6 long spines in the center. The antenna is a simple long process with spinules along its distal two-thirds and a minute pro-

cess representing the exopod which bears a single hair. The megalopa is common in the plankton, and is greenish spotted with pink chromatophores, the carapace measuring 4 mm. in length. Thus it is large compared with the first zoea. The fifth pair of legs end in 3 long feelers. The front of the carapace bends down as a rounded process. There is no true rostrum and there are no spines on the carapace. The uropods bear 19 spines. The first young crab from the megalopa measures 4 mm. across the carapace. It is very like the adult.

***Pachygrapsus transversus* (Gibbes).**

(Text-fig. 5).

This species is very common under stones on the shore above high water mark, sometimes in the water slightly lower down. All along the Reach and along the south shore of Long Bird Island it is abundant. It breeds from April to October. The eggs measured 0.28 mm. across and were hatched June 25, 1938, and later. The first zoea



TEXT-FIG. 4. *Planes minutus*. **a.** Side view of first zoea, 1.1 mm. long. **b.** Abdomen and telson. **c.** Cast skin of megalopa, carapace 4 mm. long. **d.** Abdomen. **e.** Uropod. **f.** Chela. **g.** Carapace from side. **h.** Carapace of first young crab from megalopa.

measured 0.9 mm. in length, and was green with much black. It is very like *Planes* and of the same type but is smaller and has a shorter and straighter dorsal spine. Cano (1891) describes and Hyman (1922) quotes his description of the zoeae and megalopa of *Pachygrapsus marmoratus* which in appear-

ance is very like the present species. It differs however in the telson and in having no knobs on the third abdominal somite. Two megalopae are described as belonging to *P. marmoratus*, but one cannot be certain if these really were two stages as no moults were obtained. Only one megalopa stage was

found in the Plymouth Brachyura (Lebour, 1928) but several workers have stated that two occur from other parts of the world and Aikawa (1937) notes them in *Plagusia*.

***Goniopsis cruentatus* (Latreille).**

The Mangrove Crab is very common in rock crevices above but near water. Two females were obtained in berry, Aug. 29, 1938, from rocks around the fish-pond in the Station grounds. This pond is connected with the sea. The eggs were dark brown, appearing black in bulk, and measured 0.32 mm. across. Unfortunately they did not hatch, as it was difficult to keep them alive.

***Percnon gibbesii* (Milne Edwards).**

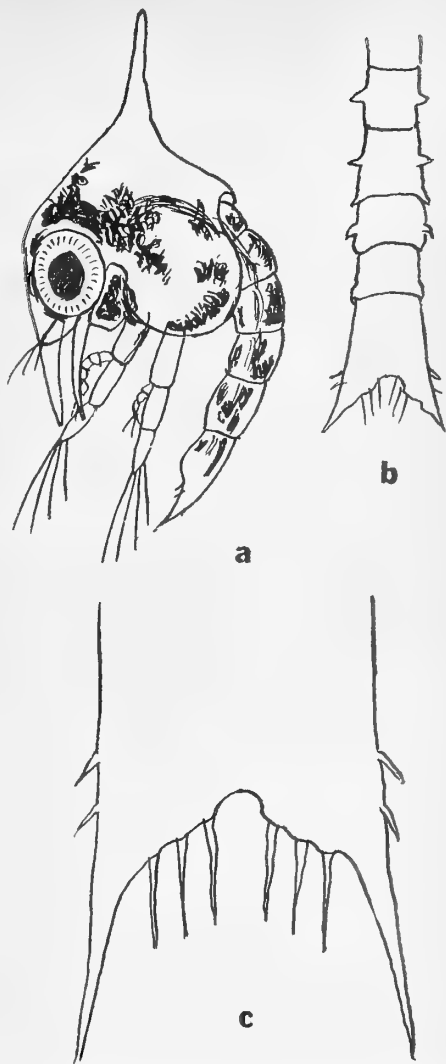
(Text-fig. 6).

This crab is common under stones on the south shore of Long Bird Island and on the other islands near. It runs very fast when disturbed and usually lives very near high water mark. It was in berry in July and some eggs were hatched July 15, 1938, but the zoeae died and the color was not noted. The eggs were bright red and measured 0.36 mm. across. The first zoea measured 1.9 mm. in length. It differs very much from *Planes* and *Pachygrapsus* but is somewhat similar to *Plagusia dentipes* described by Aikawa (1937), although differing in several points. Thus they both have lateral spines on the carapace but the antenna differs and there are knobs on abdominal somites 2-4 in *Plagusia* as there are in *Planes* and *Pachygrapsus*, while in *Percnon* they are only on 2 and 3. The telson in both *Plagusia* and *Percnon* has no lateral spine, while in *Planes* and *Pachygrapsus* there are 2. *Percnon* differs from all zoeae so far known in having the posterior part of the carapace bent up to form a flange on each side. The antenna has a minute unarmed knob representing the exopod. There is a very large and swollen anal papilla.

A megalopa of this species found by Mr. John Armstrong of Harvard University among rocks on Cooper's Island is interesting as it is very large, the carapace measuring 5 mm. in length. It has the abdomen outstretched and the uropods of a typical megalopa armed with 22 setae, but the last legs end in denticulate dactyls without any feelers, thus resembling a Spider Crab. There are 3 large teeth in front of the carapace and the walking legs are very long. It is possible that this is a megalopa in the second stage.

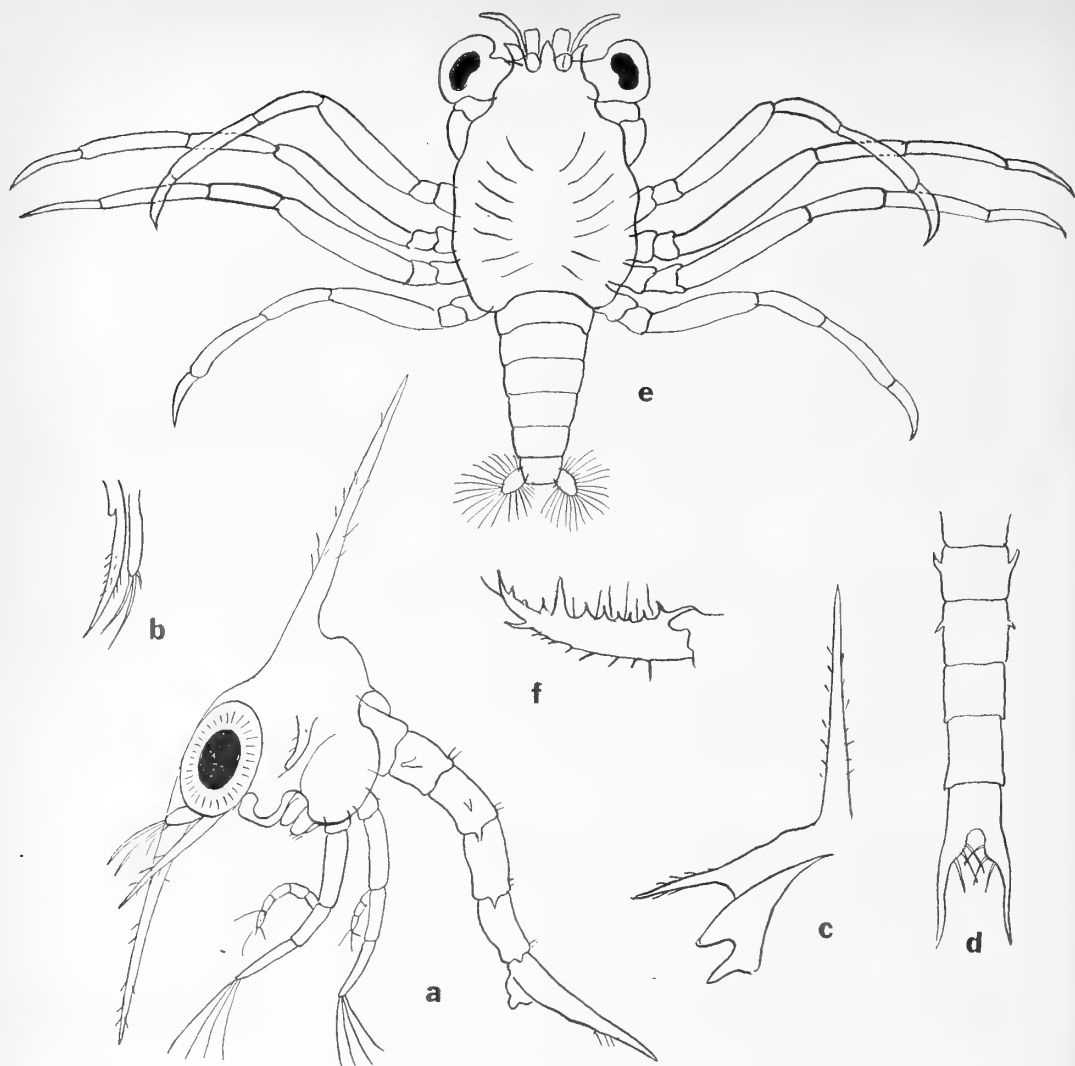
**XANTHIDAE.**

Gurney (1938 a) discusses the known zoeae of the family and shows that the characters used for the grouping of these (antennal exopod, lateral spines on the telson and spines on the carapace) do not corre-



TEXT-FIG. 5. *Pachygrapsus transversus*. **a.** Side view of first zoea, 0.9 mm. long. **b.** Abdomen and telson. **c.** Telson.

spond with the present arrangement of the adults. Three more zoeae from Bermuda can now be added to this list (Gurney, 1936 d, having already described the first zoeae of *Heteractaea ceratopus*)—*Panopeus bermudensis*, *Leptodius parvulus* and *Xanthodius denticulatus*. Of these the first two have the antennal exopod as long as the spine and the third has a short exopod with 2 terminal setae and appears to be a typical zoea of the sub-family Xanthinae. There are six known zoeae of this family which have the antennal exopod as long as, or very nearly as long as, the spine and no terminal setae. These are *Pilumnus hirtellus* (described by Lebour, 1928), *P. minutus* and *P. vespertilis* (described by Aikawa, 1929), *Panopeus ber-*

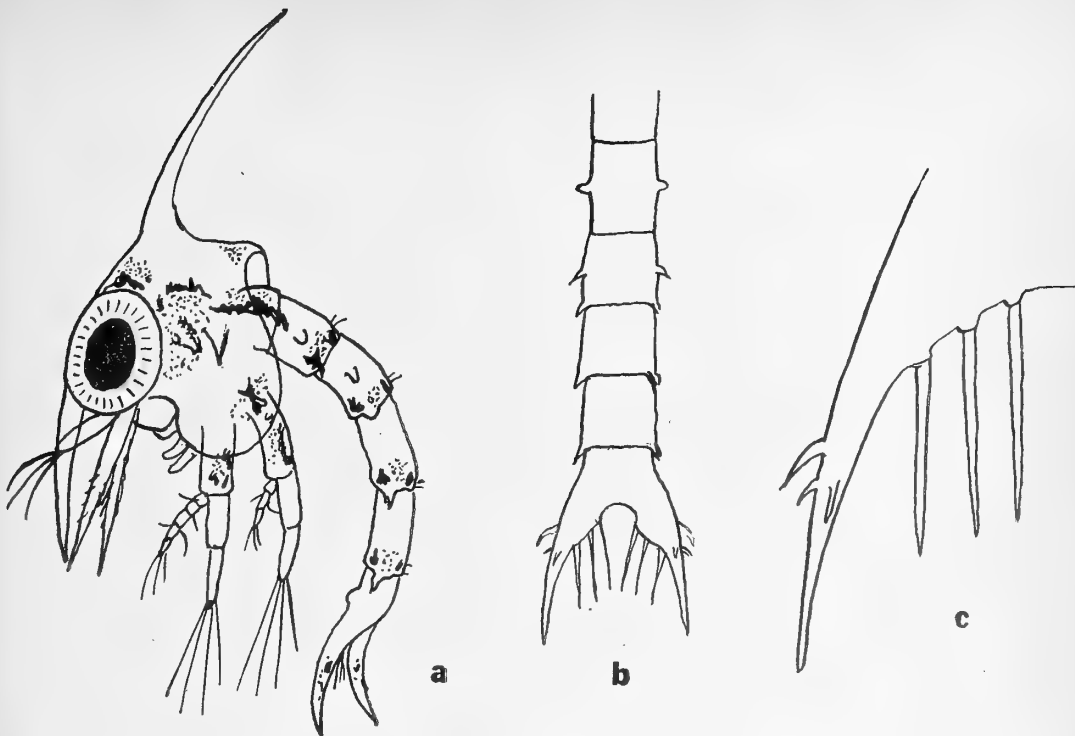


TEXT-FIG. 6. *Percnon gibbesii*. **a.** Side view of zoea, 1.9 mm. long. **b.** Antennule and antenna. **c.** Posterior end of carapace. **d.** Abdomen and telson. **e.** Megalopa. **f.** End of last leg.

*mudensis* and *Leptodius parvulus* (described here) and *Heteropanope glabra* (described by Aikawa, 1929). Cano (1892 c) describes three species of *Pilumnus* including *P. hirtellus* but does not differentiate between them. These are quoted by Hyman (1925) and are all of the same type as *hirtellus*. The *Pilumnus* species (excepting those of Cano) were all hatched from the egg and agree except for the fact that *P. minutus* has only 2 lateral spines on the telson instead of 3. They all have 3 kinds of spines on the carapace. *Leptodius parvulus* agrees with *Pilumnus hirtellus*. *Heteropanope glabra* lacks the dorsal and rostral spines on the carapace and has only one lateral spine on the telson. *Panopeus bermudensis* comes

between the *Pilumnus* species and *Heteropanope glabra*, having very short rostral and lateral spines on the carapace, as in *Pilumnus minutus*, but agreeing with *Heteropanope glabra* in having only one lateral spine on the telson. These 6 species seem to form a group characterized by the antenna as opposed to all the remaining zoeae known in the family which have the exopod shorter than the spine, either vestigial or with terminal setae. As Gurney (1938 a) points out, the difference between the zoeae of *Heteropanope glabra* and *H. tridentata* (the latter described by Tesch, 1922) is so striking that if the description and parentage are correct any classification according to larval characters on these lines is upset.





TEXT-FIG. 7. *Leptodius parvulus*. **a.** Side view of first zoea, 1.12 mm. long. **b.** Abdomen and telson. **c.** Telson.

***Leptodius parvulus* (Fab.) Rathbun.**  
(Text-fig. 7).

The zoea is of the *Pilumnus* type but in form and color is very like that of *Xanthodius denticulatus* described below. This species is common in rocks and under stones between tide-marks on the south shore of Long Bird Island. In berry in June. The eggs were hatched July 2, 1938, and were brown, 0.32 mm. across. The newly hatched zoea measures 1.12 mm. in length. It is a pale grayish-blue all over; it is not so transparent as *Xanthodius denticulatus*, with rather more red and black pigment, which besides being on the thorax and abdomen also occurs on the maxillipedes and horns of the telson. There are dorsal, rostral and lateral spines on the carapace, all well developed, the dorsal and rostral being long. There are 3 lateral spines on the telson and knobs on abdominal somites 1 and 2. The antennal exopod is as long as the spine and has no terminal setae.

***Panopeus bermudensis* Benedict & Rathbun.**  
(Text-fig. 9).

This species was dredged off the north shore of Long Bird Island and was in berry June 10, 1938. The eggs measured 0.32 mm., very red. They were hatched June 14. The

newly hatched zoea, 1.4 mm. long, is greenish with black chromatophores and at first sight looks very like *Planes minutus* and *Pachygrapsus transversus*. It is peculiar and unlike other xanthid zoeae in having spine-like knobs on the fourth and fifth abdominal somites as well as on the second and third. There are denticulations posterolaterally on the carapace and only one lateral spine on the telson. The antennal exopod is as long as the spine.

***Panopeus occidentalis* Saussure.**

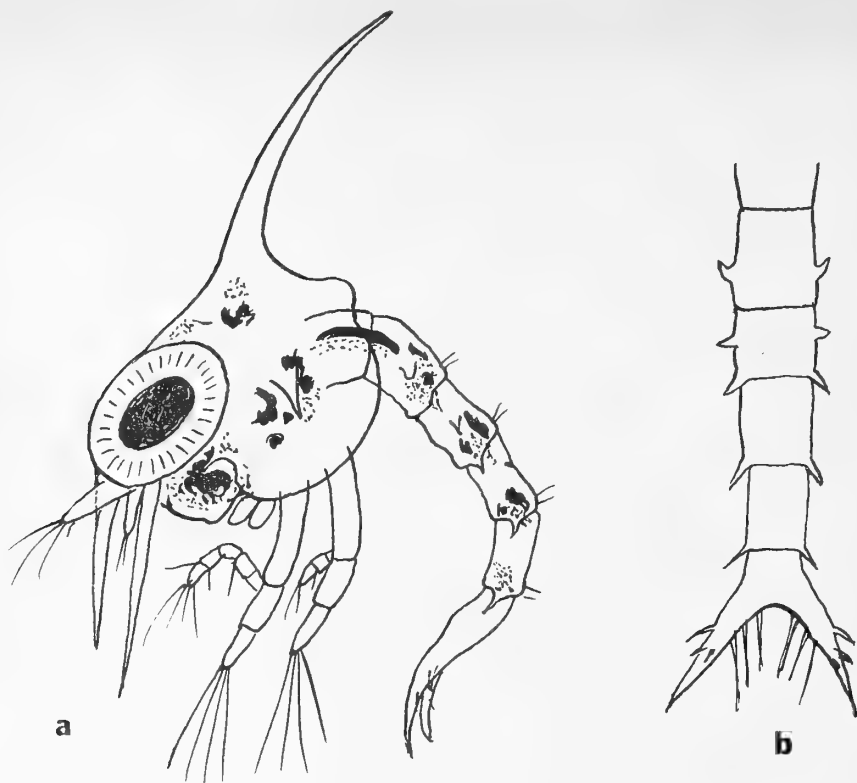
From Spanish Point. In berry Aug. 11, 1938. The eggs were black, 0.32 mm. across. The crab died and the eggs were not hatched.

***Micropanope spinifer* Milne Edwards.**

From a rock crevice on the south shore of Long Bird Island. In berry June 20, 1938. The eggs were dark red, 0.32 mm. across. The crab died and the eggs did not hatch.

***Xanthodius denticulatus* (White) Rathbun.**  
(Text-fig. 8).

This crab was obtained fairly commonly on the south shore of Long Bird Island and was in berry in July. The eggs were hatched out July 24 and July 26, 1938, and measured



TEXT-FIG. 8. *Xanthodius denticulatus*. **a.** Side view of first zoea, 1.3 mm. long. **b.** Abdomen and telson.

0.34 mm. across when ready to hatch. The newly hatched zoea measured 1.3 mm. in length and was very transparent with black and red chromatophores on the thorax and abdominal somites and in the region of the mandible. The antennal exopod is about a quarter the length of the spine, with 2 terminal setae. The dorsal and rostral spines are fairly long and of about equal length, the lateral spines short. The telson has the usual 3 outer spines. There are lateral spines on abdominal somites 3-5 and lateral knobs on 2-3. This appears to be of the *Xantho* type.

## OXYRHYNCHA.

### MAJIDAE.

The crabs hatched out belong to the sub-families Acanthonychinae: *Acanthonyx petiverii*, and Majinae: *Mithrax forceps* and *Microphrys bicornutus*. The zoea of the first is like that of *Acanthonyx lunula* described by Cano (1893 b) and Boraschi (1921), the other two come between the *Pisa* type of zoea (Lebour, 1931 c) and that of *Maia* (Lebour, 1927 and 1928 b).

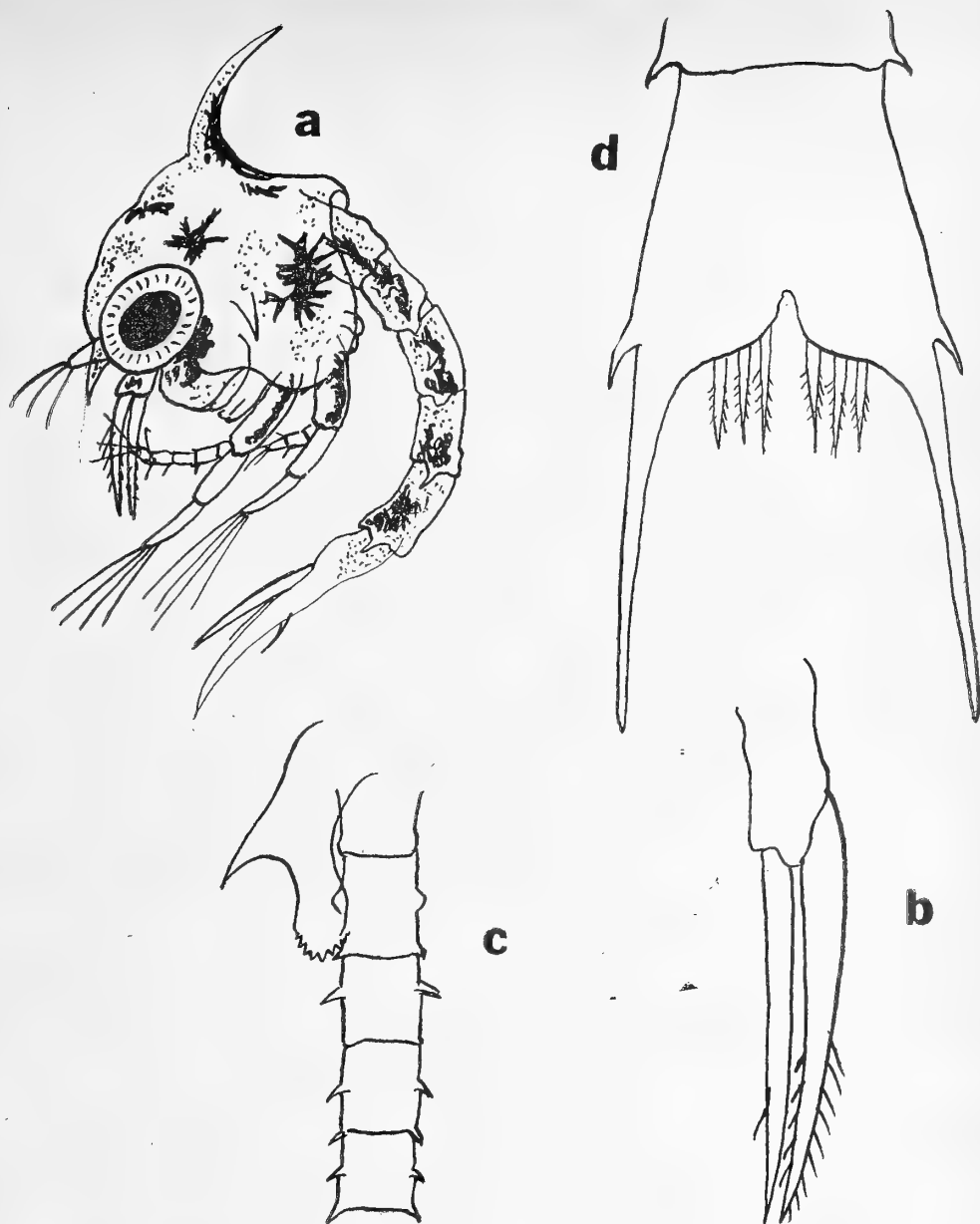
*Acanthonyx petiverii* Milne Edwards.  
(Text-fig. 10).

These crabs are abundant, living among

seaweeds (including *Fucus*) in rocky pools around Cooper's Island and one was dredged in sand just outside it. I am indebted to Dr. F. A. Chace, Jr., for its identification. The seaweed appears to be the natural habitat as they have pieces of the weed on the rostrum and sometimes about the body and closely resemble the weed itself. This is a new record for Bermuda. Females in berry were obtained in April and the zoeae hatched out May 2, 1939. The newly hatched zoea measures 1.8 mm. in length and corresponds in form with that of *Acanthonyx* described by Cano (1893 b), having a short dorsal spine, a very short rostral spine and no lateral spines, no lateral spines on the telson and the antennal exopod as long as, or slightly longer than, the spine, with no terminal setae, but 2 setae near the tip. There are knobs on the second abdominal somite. The body is a pale pinkish-brown with much black pigment, especially in the thorax and ventrally on each abdominal somite. The early eggs were golden yellow, 0.56 mm. across, the later eggs slightly larger and appearing black in the mass.

*Epialtus bituberculatus* Milne Edwards.

This crab was dredged from sand off Cooper's Island with *Acanthonyx* and was also obtained by Dr. Klitemann in Hungry



TEXT-FIG. 9. *Panopeus bermudensis*. a. Side view of first zoea, 1.4 mm. long. b. Antenna. c. Abdomen d. Telson.

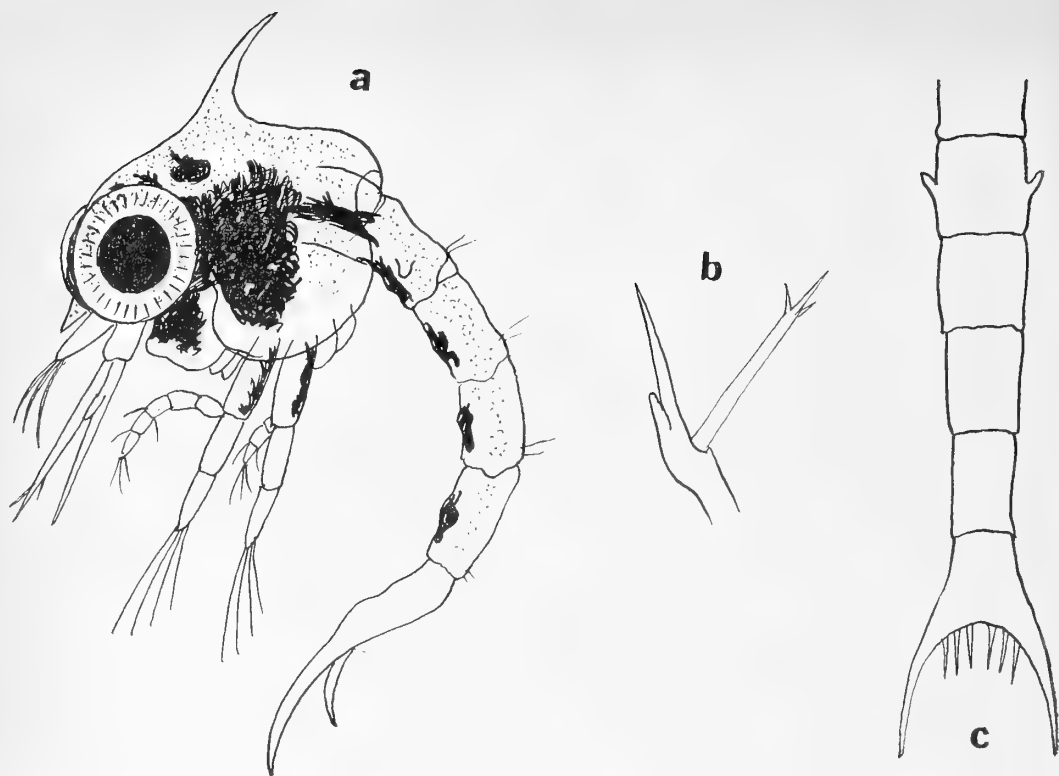
Bay, in berry, both in April. Unfortunately the eggs did not hatch, as the crabs died. The eggs are few and large, 0.72 mm. across, pinkish with a bright orange-red yolk.

***Mithrax forceps* Milne Edwards.**

(Text-fig. 11).

This crab occurred not uncommonly on the south shore of Long Bird Island and Tobacco Bay near St. Georges, in rocks between tide-marks. In berry in July. The

eggs hatched July 6, 1938, and were 0.64 mm. across and dark brown. The newly hatched zoea measured 1.8 mm. in length. The dorsal spine is short, the rostral very short, and there are no lateral spines. There is one lateral spine on the telson, the forks of which bear spinules, and there is a pair of lateral knobs on the second abdominal somite. The antennal exopod is not quite as long as the spine and bears 3 terminal setae. There are lateral spines on the third, fourth and fifth abdominal



TEXT-FIG. 10. *Acanthonyx petiverii*. **a.** Side view of first zoea, 1.8 mm, long. **b.** Antenna. **c.** Abdomen and telson.

somites. Thus in the type of antenna it resembles *Maia* but in most of its other features it is more like *Pisa*. The color is pale yellowish with pink on the abdomen and on the maxillipedes, black in the thorax and in patches on the abdominal somites.

***Microphrys bicornutus* (Latreille).**

(Text-fig. 12).

This crab is common under stones along the shore between tide-marks and was obtained from the north and south shores of Long Bird Island and from a sandy bay on St. David's Island. In berry June and July. The eggs, 0.48 mm. across and dark brown, were hatched June 29, 1938. The zoea is very like that of *Mithrax* but the eyes are much larger and of a peculiarly vivid blue. The dorsal spine is short, the rostral very short, even shorter than that of *Mithrax*, and there are no lateral spines. There is one lateral spine on the telson, and the forks bear spinules. There are lateral knobs on the second abdominal somite and somites 3-5 have lateral spines. The antenna is like *Mithrax* except that the exopod is shorter in proportion to the spine. The body is a transparent yellow with red chromatophores behind the carapace and at the base of the second maxillipede and black on the

thorax in patches and ventrally on the abdominal somites. The first zoea changed to the second (last) in a small glass bowl. It is very little larger than the first, but the pleopods are very long and there are 6 setae on the maxillipedes.

**PARTHENOPIDAE.**

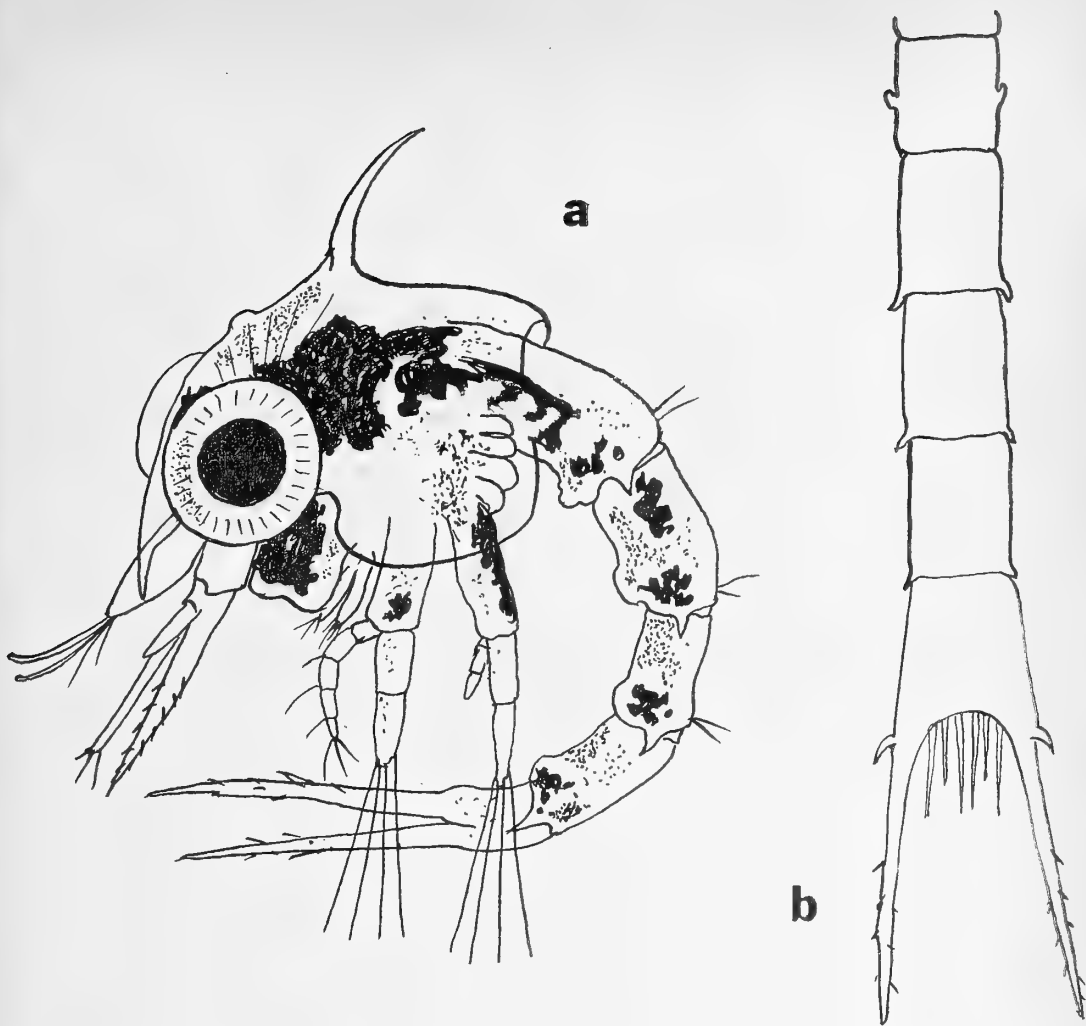
(Text-fig. 13).

The megalopa of a species of *Parthenope* was occasionally taken in the outside tow-nets. This had a characteristic form with very long chelae. The carapace, including rostrum, measured 3.5 mm. in length. There is a long dorsal and a long rostral spine, the abdominal somites 3-5 have lateral spines and the uropods bear numerous setae (exact number not ascertained). As is found in all the known megalopae of the Oxyrhyncha, there are no feelers on the dactyl of the last leg, but this is armed with teeth and hairs.

**OXYSTOMATA.**

**LEUCOSIIDAE.**

Several undetermined zoeae of *Ebalia*-like form were obtained in the outside tow-nets, one of which was occasionally abundant. Three species, A, B and C, were distin-



TEXT-FIG. 11. *Mithrax forceps*. **a.** Side view of first zoea, 1.8 mm. long. **b.** Abdomen and telson.

guished. All of them had much black pigment on the body.

*Species A* (Text-fig. 14). This was much the commonest. There was much heavy black pigment in the thoracic region. There are long dorsal and rostral spines and fairly conspicuous lateral spines. The second and third abdominal somites have lateral knobs and the telson has one lateral tooth near the angle. The first zoea measured 0.80 mm. in length; the third, which had 6 setae on the maxillipedes, and fairly conspicuous pleopods, measured 1.9 mm., and the fourth (last) measured 3 mm. The last had 8 setae on the maxillipedes and very long pleopods.

*Species B* (Text-fig. 15). Has a fairly long dorsal spine (broken in the figure), a short rostral spine and no lateral spines. This measured ca. 2.2 mm. in length in the last stage. The telson is similar to A.

*Species C* (Text-fig. 16). Measured 2.2 mm. in length in the second stage and is like B but with a longer rostral spine and no outer spine to the telson.

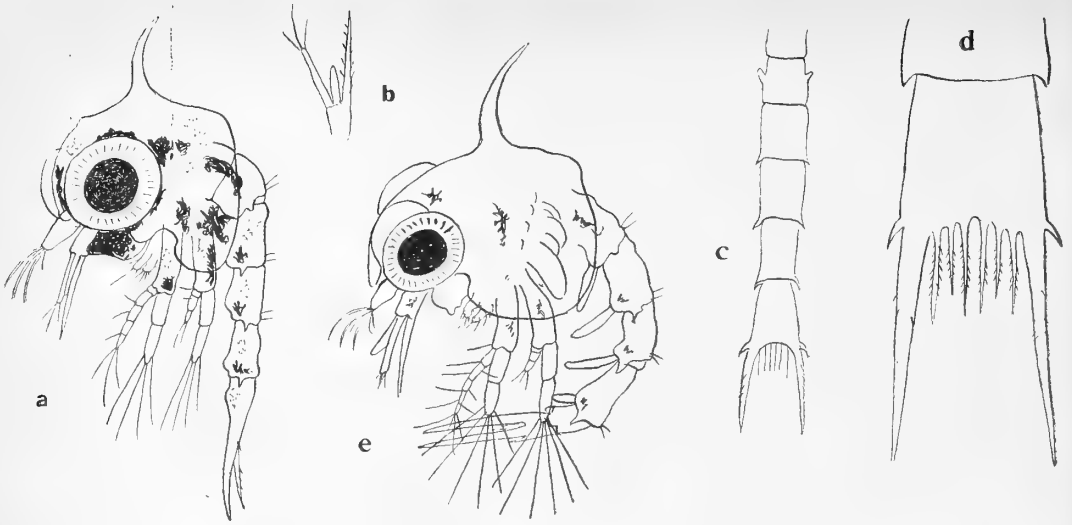
It is worth while recording these forms, as species belonging to this family are extremely rare in Bermuda and probably several have yet to be found there.

#### CALAPPIDAE.

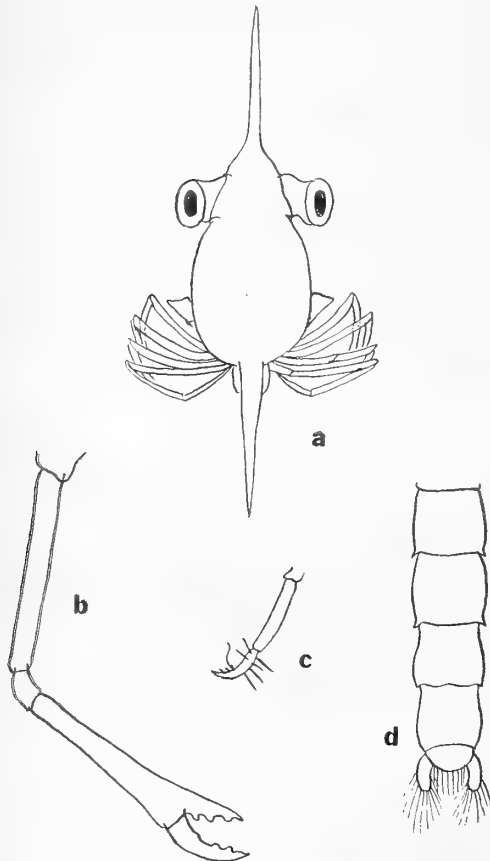
##### *Calappa flammea* (Herbst).

(Text-fig. 17).

The megalopae of this species have already been described by Smith (1880 b, as *Calappa marmorata*), but not figured. They are found occasionally on the outside townets and swimming at the surface in the shallow water of the Reach at night, the adult being common around the coasts. A



TEXT-FIG. 12. *Microphrys bicornutus*. **a.** Side view of first zoea, 1.7 mm. long. **b.** Antenna. **c.** Abdomen and telson. **d.** Telson. **e.** Side view of second zoea.



TEXT-FIG. 13. *Parthenope* sp. **a.** Megalopa carapace, 3.5 mm. long. **b.** Chela. **c.** End of last leg. **d.** Abdomen and telson.

peculiar and striking feature of this megalopa, not noted by Smith, is the presence of very large oil-like spherical globules in the thoracic region, always 12 in number. Although they may be arranged in a slightly different manner they are always symmetrically placed. The body is a pale yellowish all over. There are 20 setae on the uropods, and, as Smith has pointed out, there are 3 feelers on the end of the dactyl of the last leg. This changed to a young crab, June 21, 1938. The carapace measured 4.2 mm. across. The specimen died and was slightly damaged, therefore the drawing shows the carapace distorted. A specimen from deeper water, presumably the same species, differs slightly from the others (Text-fig. 18).

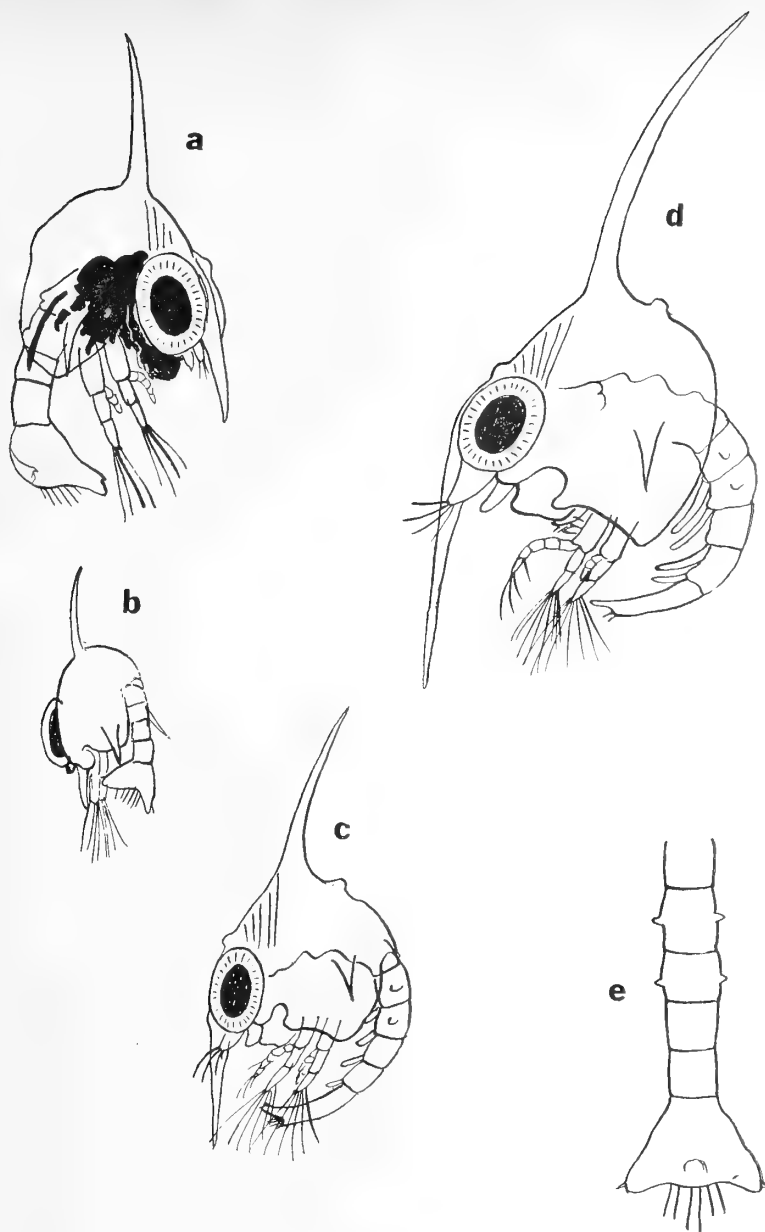
#### *Cycloës bairdii* Stimpson.

(Text-fig. 19).

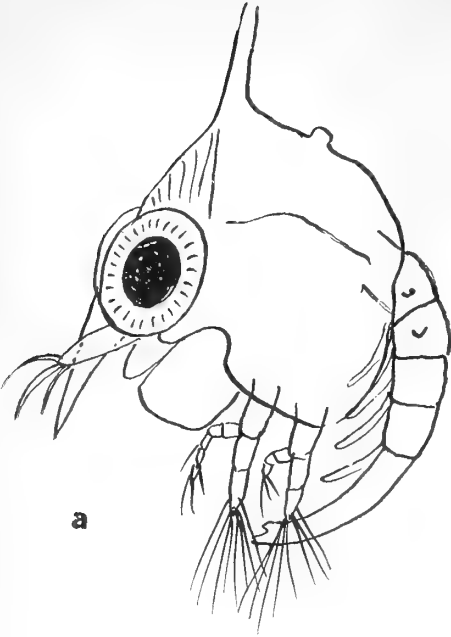
The megalopa, hitherto undescribed, of this species, which in many ways resembles that of *Calappa*, was obtained occasionally in the outside tow-nets. It is pale yellow all over with small red spots. The carapace measured 3 mm. long and is rather narrower than that of *Calappa*. There are here also large globules in the thorax but there are 14 of them. The last leg ends in 3 feelers. The uropods bear 17 setae. There are tubercles on the dactyl of the chela and along the propodus. This changed to a young crab which has a very round carapace, measuring 3 mm. in length. The chelae are of the characteristic shape of the adult.

#### BIBLIOGRAPHY.

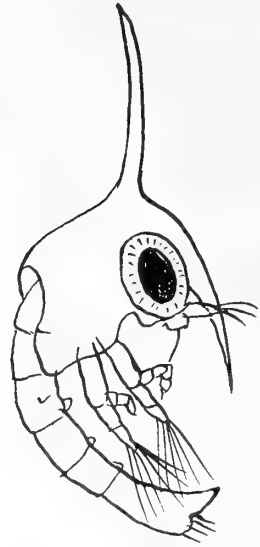
The literature is all referred to Gurney's Bibliography of the Larvae of Decapod Crustacea. 1939. Ray Society.



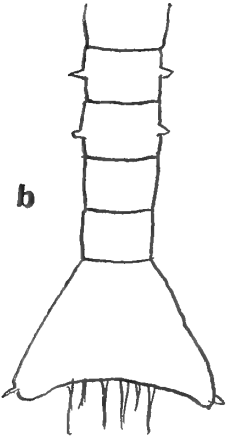
TEXT-FIG. 14. *Ebalia*-like zoea A. **a.** Side view of Species A, 0.8 mm. long. **b.** Back oblique view. **c.** Stage 3. **d.** Stage 4 (last). **e.** Abdomen and telson of stage 4.



**a**

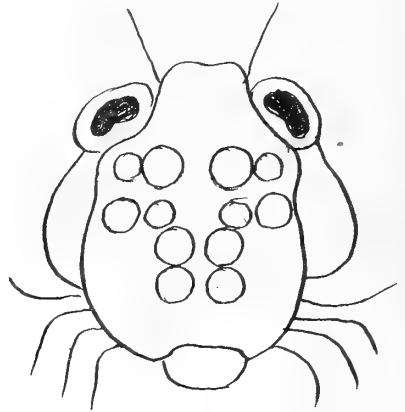


TEXT-FIG. 16. *Ebalia*-like zoea C, second (?) stage, 1.5 mm. long.



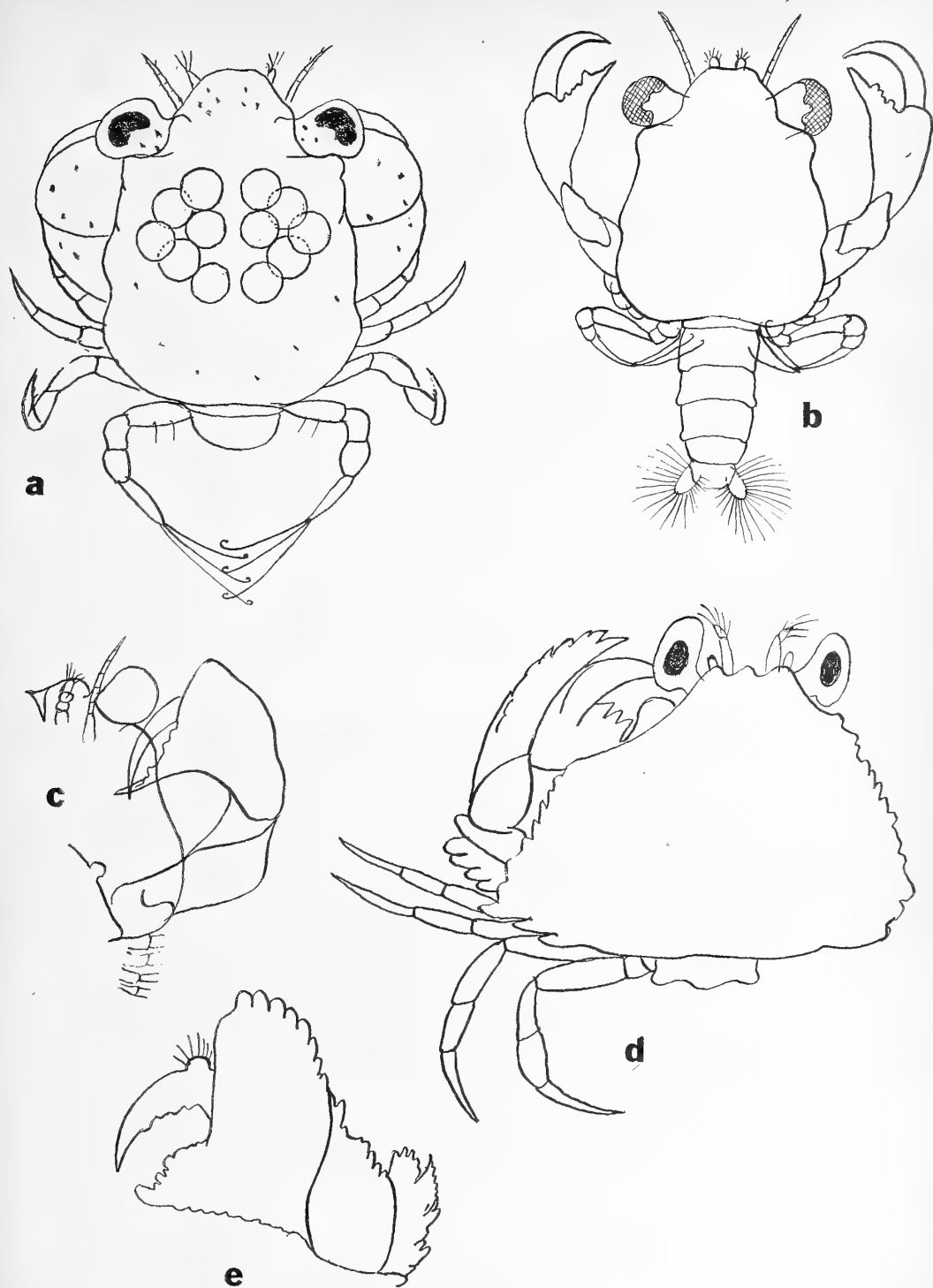
**b**

TEXT-FIG. 15 *Ebalia*-like zoea B. **a.** Side view of last stage, 2.2 mm. long. **b.** Abdomen and telson.

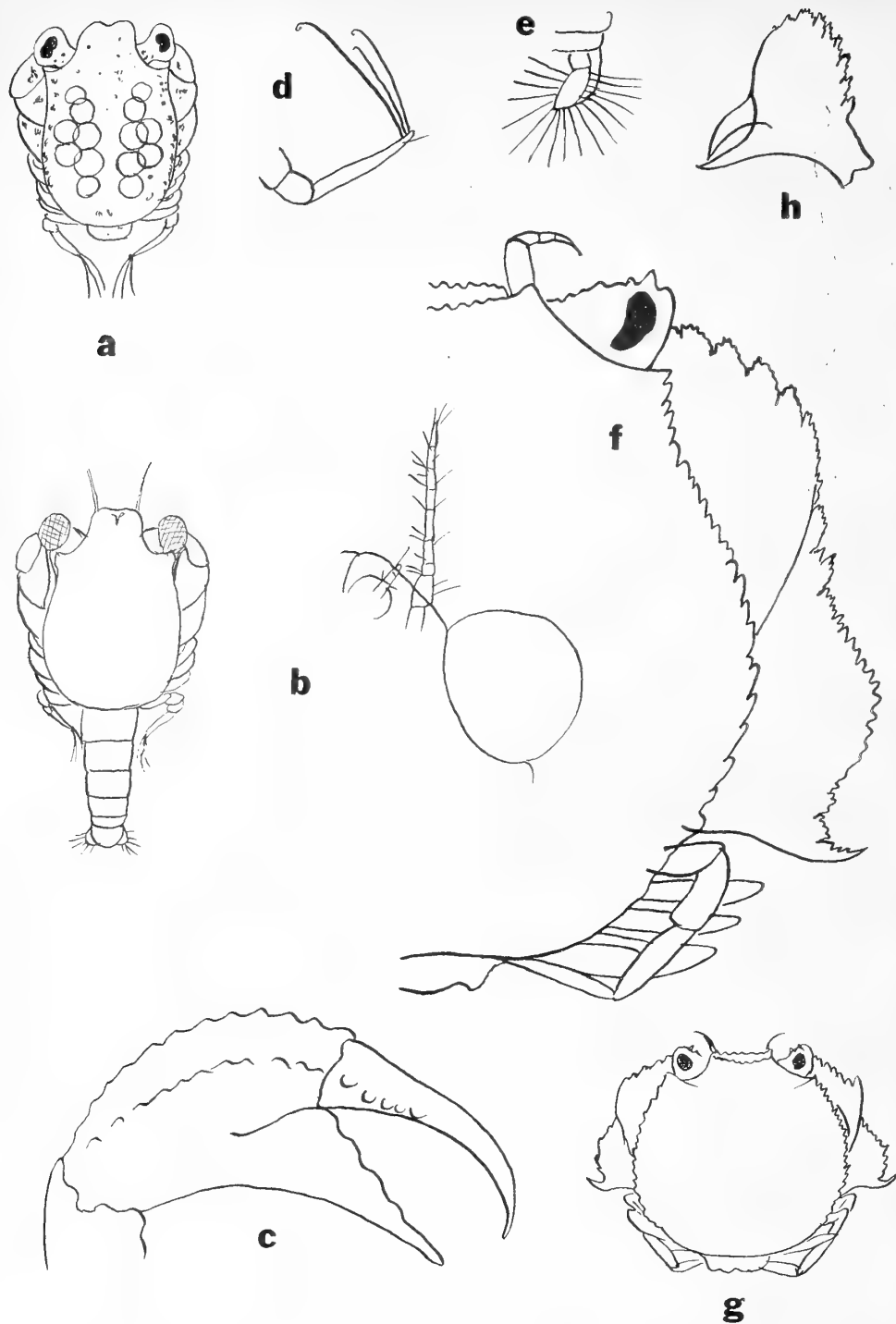


TEXT-FIG. 18. Rough sketch of another megalopa from deeper water.





TEXT-FIG. 17. *Calappa flammea*. **a.** Megalopa, 4.5 mm. long. **b.** Cast megalopa, dorsal. **c.** Cast megalopa, ventral. **d.** First crab from megalopa, carapace 4.2 mm. long. **e.** Chela.



TEXT-FIG. 19. *Cycloës bairdii*. **a.** Megalopa, carapace 3 mm, long. **b.** Cast megalopa. **c.** Chela. **d.** End of last leg. **e.** Telson and uropod. **f.** **g.** First crab from megalopa, 3 mm long. **h.** A chela.

## 12.

Some Venezuelan Aquatic Hemiptera.<sup>1</sup>

H. B. HUNGERFORD

University of Kansas.

[This is a contribution from the Forty-third or Venezuelan Expedition of the Department of Tropical Research of the New York Zoological Society made under the direction of Dr. William Beebe. The expedition was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

By the courtesy of Dr. William Beebe I have been permitted to examine a small collection of aquatic hemiptera from Caripito, Venezuela. In the matter of distribution this list is of importance, as eight out of the eleven species have not heretofore been recorded from Venezuela.

1. *Lethocerus grandis* (Linn.).

Brazil, Paraguay, Colombia. A new record for Venezuela.

2. *Lethocerus annulipes* H.S.

U.S.A. (Florida), Mexico, Honduras, Guatemala, Nicaragua, Costa Rica, Panama, Cuba, Jamaica, Colombia, Venezuela, British Guiana, French Guiana, Puerto Rico, Paraguay, Uruguay, Brazil, Argentina.

3. *Lethocerus mello-leitaoi* DeCarlo.

Brazil, Paraguay. A new record for Venezuela.

4. *Belostoma dentatum* (Mayr).

Venezuela, Bolivia, Brazil, Argentina, Paraguay.

5. *Belostoma asiaticum* (Mayr).

Mexico, Peru, Argentina, Brazil. A new record for Venezuela.

6. *Tenagogonus duolineatus* Kuitert.

Bolivia, Peru, Paraguay. A new record for Venezuela.

7. *Limnogonus celeris magnus* Kuitert.

Bolivia, Brazil, British Guiana. A new record for Venezuela.

8. *Potamobates unidentata* Champion.

Panama, Colombia. The Venezuela specimen has a different color pattern and must be at least a new variety.

9. *Rhagovelia insularis* Champion.

Trinidad, Brazil, Colombia, Panama. A new record for Venezuela.

10. *Rhagovelia tenuipes* Champion.

Mexico. A new record for Venezuela.

11. *Ranatra macrophthalma* H. S.

Colombia, Peru, Bolivia, Dutch Guiana, French Guiana, Brazil, Venezuela.

<sup>1</sup> Contribution No. 693, Department of Tropical Research, New York Zoological Society.



## 13.

Ocular Anatomy and Light Sensitivity Studies on the Blind Fish  
from Cueva de los Sabinos, Mexico.

C. M. BREDER, JR.

*The American Museum of Natural History*

(Plate I; Text-figures 1-3).

## INTRODUCTION.

The discovery of another blind characin from the Mexican caves of the State of San Luis Potosi, which is advanced beyond the conditions of eye degeneration found in the specimens of La Cueva Chica, calls for an examination of this new form in regard to its ocular anatomy and reactions to light. The present contribution is thus a continuation of the studies of Gresser & Breder (1940) and Breder & Gresser (1941a, b and c).

The finding of this fish, under taxonomic study by Dr. C. L. Hubbs, has been reported by Tafall (1942 and 1943). This second cave, Cueva de los Sabinos, is about fifteen miles distant from La Cueva Chica. Chemotropic reactions of this fish, the La Cueva Chica specimens and the deriving river fish, *Astyanax mexicanus* (Philippi), have been reported by Breder & Rasquin (1943). The current status of the whole problem and a preliminary notice of some of the conclusions of the present paper have been given by Breder (1943c).

The experimental part of the study has been carried on in the Department of Animal Behavior of the American Museum of Natural History. The histological sections of the head have been made by Miss Priscilla Rasquin. The cleared and stained skulls have been prepared by Miss A. M. Holz. Dr. Ralph Meader, of Yale University, examined and interpreted certain of the sections and provided the photographs of Plate I. Dr. W. K. Gregory gave advice in connection with interpretation of the osteological changes. Dr. E. B. Gresser, of New York University, gave helpful aid in connection with the comparisons of the ocular details. To all of these people the author wishes to express his grateful appreciation.

## STRUCTURE OF THE EYE.

Compared with the eye remnant of the fishes from La Cueva Chica, described by

Gresser & Breder (1940) and Breder & Gresser (1941a), the optical architecture of the fishes from Cueva de los Sabinos is still further reduced. Hardly anything is left of the eye capsule found in the more advanced of the mixed fishes from La Cueva Chica. In addition to this great reduction of the capsule there is no optic nerve connecting with the brain.

Unsatisfied with the difficulties in finding and interpreting these remnant structures, the slides were referred to Dr. Ralph Meader of Yale University who is engaged in studying the brain tracts of these fishes. His careful examination of the slides brought out numerous fine details about which he wrote as follows, for inclusion in this paper.

"An optic capsule is present embedded in the fat which fills the region of the head normally occupied by the eye and orbit in eyed river fish. The capsule consists of a sphere of moderately heavy cartilage, incomplete on its medial wall where it is replaced by a lamina of dense connective tissue. Within the capsule is a more or less loose network of connective tissue in which lies a small heavily pigmented sphere or cyst, which presumably represents the choroid coat. Although some stainable material is visible within this cyst and it contains some cells of unidentified origin, no recognizable elements of a retina can be found. There is no lens nor any of its associated structures. Outside of the pigmented sphere are a few vascular channels which are probably the remnant of the choroidal gland. A few strands of striated muscle are seen in the region of the connective tissue which completes the medial wall of the cartilaginous outer layer of the capsule. The muscle fibers do not show well the normal histology of voluntary muscle. Near them, attached to one capsule, can be seen a small bundle of tissue which in its shape and position resembles the atrophic optic nerves of some blind specimens from La Cueva Chica. The bundle can be traced medialward only a short

distance from the capsule before it becomes very small and then ends. No similar bundle can be seen attached to the other capsule.

"From the anterolateral aspect of each optic capsule a stalk of tissue extends towards the skin. On one side this stalk is small and hollow near the capsule. A few cells with large nuclei line the cavity which is filled with amorphous debris. Nearer the skin the stalk becomes smaller and solid. Its final attachment cannot be certainly made out because of torn sections, but it probably attaches to the connective tissue underlying the skin that covers over the obliterated orbital cavity. On the opposite side of the head, the stalk is relatively large, hollow, and has definite attachment to the skin. The same type of cells with large nuclei lines its cavity and the cells which form the rest of its thick wall resemble somewhat those of the skin. At one place they nearly become continuous with the surface epithelium. These stalks resemble those described by Gresser & Breder (1940) and Breder & Gresser (1941a) for the blind fish from La Cueva Chica. They are most like that shown in their figure 2 (1941a).

"The condition of this optic capsule in the Sabinos fish seems to be an exaggeration of the reduction in size and in the loss of retina seen in occasional specimens from La Cueva Chica. For example one of the latter specimens prepared here exhibits no retinal structure although in one pigmented cyst is evident a multipolar nerve cell whose presence I cannot explain. This specimen, however, does have an optic nerve that can be traced to the brain whereas in the Sabinos specimen, no optic nerve can be certainly identified and the strand tentatively named the optic nerve peters out in the orbital fat. No optic nerve can be found connected with the brain."

Plate I shows sections illustrating the above description and is comparable to the plates in Breder & Gresser (1941a) of the La Cueva Chica material, and taken together they clearly indicate the increasing reduction of architectural detail.

#### MODIFICATIONS OF THE SKULL.

With such a reduction of the eye it is to be expected that the osteological elements surrounding this area should show some modification. These include progressive changes accompanying the reduction of the globe and involve conspicuously a closing in of the circumorbital series of bones. The details of these changes in the conformation of the skull are indicated in Text-figure 1, which has been based on

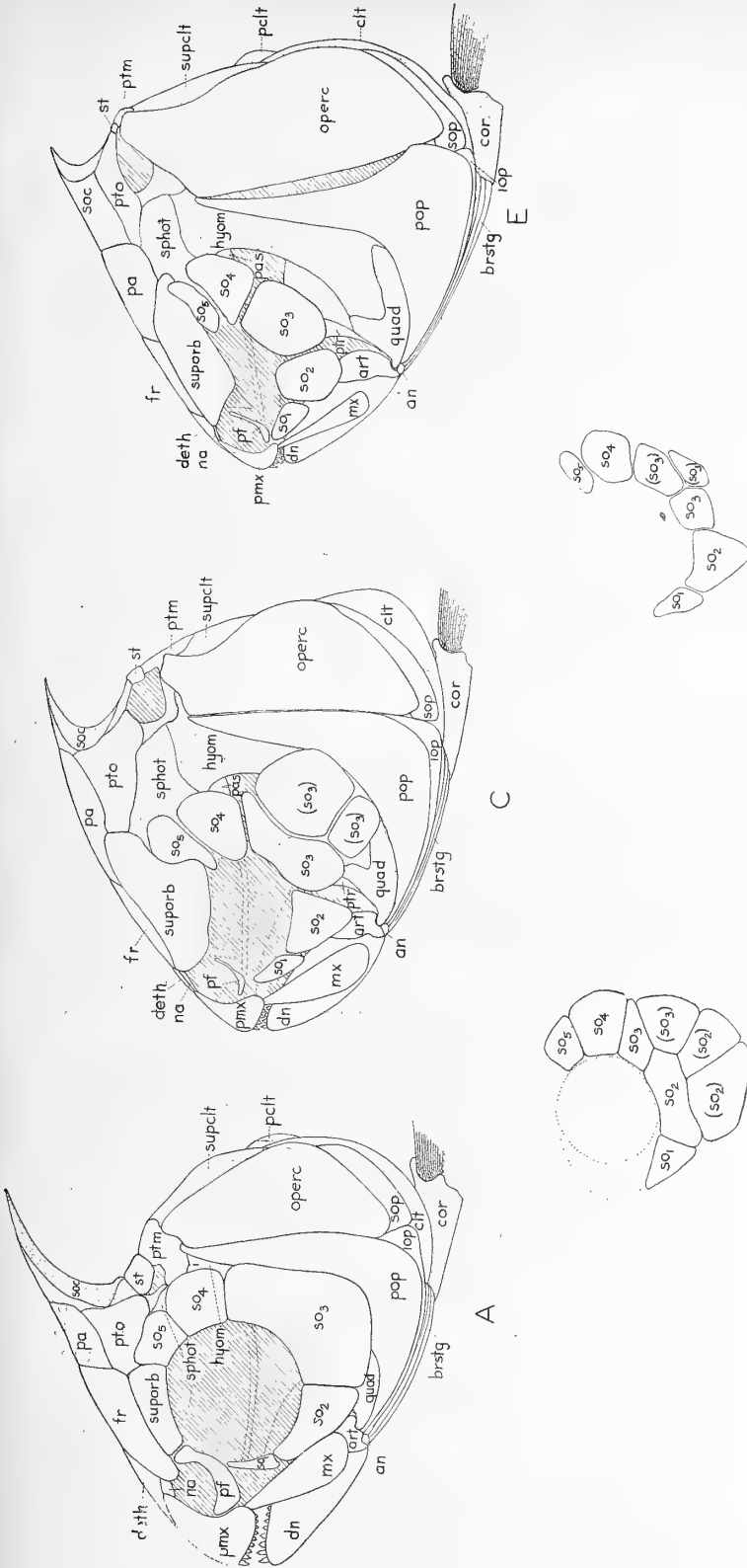
camera lucida drawings of cleared and stained heads. The sutures in the outer series of bones were easily evident, but some of the elements of the chondrocranium were discerned with difficulty or not at all, leading to the omission of certain bone names in the figure.

The normal-eyed river fish, Text-figure 1a, shows a series of five suborbital bones and a well ossified skull, as was evidenced by the taking of the stain (alizarin). This skull is a generalized type of characin skull as may be noted by a comparison with the figures of Gregory (1933) and Gregory & Conrad (1938). It resembles clearly that of *Cheirodon*, which these authors, following Eigenmann (1917), consider basic to the group containing *Astyanax* and which they designate the Cheirodontinae.

A specimen from La Cueva Chica with a reduced eye shows an essentially similar structure, but with the circumorbital series of bones closed in and with the addition of three new elements. These are evidently fragmentations of  $so_2$  and  $so_3$ , or new centers of ossification induced primarily by the shrinkage of the eye diameter. The arrangement of this series of bones is indicated in Text-figure 1b, together with the diameter of the globe and the larger anterior extension of the orbit.

A typical blind fish from La Cueva Chica shows a still further closing in of the suborbital series, with the elimination of the globe proper, Text-figure 1c, and what appears to be a fragmentation of  $so_3$  into three elements. This is one less than the number of new elements shown by the fish with merely a reduced eye diameter, and there are other changes to be discussed later. A second specimen of the same type showed a similar fragmentation of this bone, but the arrangement of the separate elements is rather different. This series of circumorbital bones is seen in Text-figure 1d. Both these fishes showed minor variations in these details from side to side. Such variations in the mixed fishes from La Cueva Chica should probably be expected in any structure associated with the features of reduction and are evidently equivalent to the variations in the eye itself already discussed by Breder & Gresser (1941a).

A specimen from Cueva de los Sabinos shows a still further closing in of the suborbital series, as is indicated in Text-figure 1e. Along with this but not indicated in the figure is an evident reduction of ossification, indicated by the manner in which the stain is retained. It will be noted that the circumorbital series has returned to five in number; thus the fragmen-



TEXT-FIG. 1. Skulls of cave fish series. **A.** Normal-eyed river fish. **B.** Circumorbital bones of perfect but small eyed specimen. The dotted lines indicate the outline of the orbit and the globe of the eye. **C.** Fully blind specimen from La Cueva Chica. **D.** Circumorbital bones of another fully blind specimen from La Cueva Chica. **E.** Cueva de los Sabinos fish. Abbreviations: **an**—angular, **art**—articular, **brstg**—branchiostegal, **clt**—cleithrum, **cor**—coracoid, **deth**—dermethmoid, **dn**—dentary, **fr**—frontal, **iop**—interopercular, **mx**—maxilla, **na**—nasal, **operc**—opercular, **pa**—parietal, **pas**—parasphenoid, **pclt**—postcleithrum, **pf**—prefrontal, **pmx**—premaxilla, **pop**—preopercular, **pftm**—posttemporal, **pfto**—pterotic, **ptr**—pterygoid, **quad**—quadrate, **so**—suborbital, **soc**—supraoccipital, **sop**—subopercular, **sphot**—sphenotic, **st**—supratemporal (scale bone), **supclt**—supracleithrum, **suporb**—supraorbital.

tation or new elements, is evidently a transient phenomenon, which reaches its highest development immediately on the reduction of the eye size and is then gradually reduced to the original state, perhaps as a new level of organizational stability is attained. This specimen, on the other side, was not so far reduced,  $so_3$  being represented by two elements which occupy an area nearly equivalent to that of the single  $so_3$  on the side illustrated.

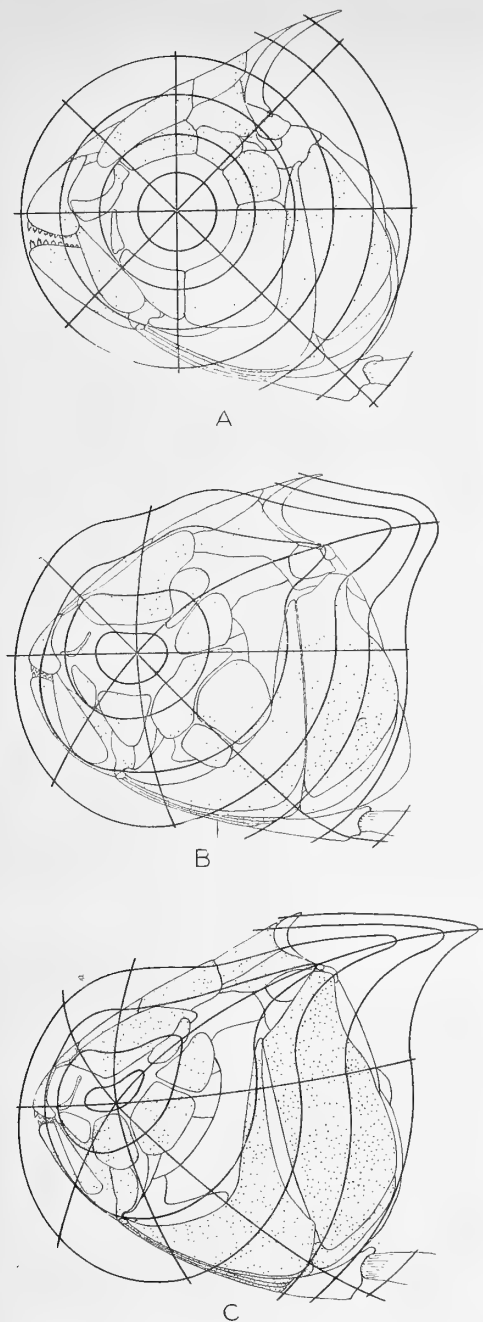
The increased exposure of the chondrocranial elements is evident from the series of three skulls in Text-figure 1, as the surface bones crowd forward as the eye is reduced. If there is any involvement of the basic nature of the jaw musculature, as found by Petit (1940) for *Typhleotris madagascariensis* Petit and *Coecobarbus geertsi* Boulenger, it is not evident from these specimens. Text-figure 1 well indicates the reduction of the size of the maxilla, premaxilla and dentary and the near loss of the prefrontal. Otherwise there is a general shifting around of all the head bones in more or less minor fashion, as they evidently spread or contract to fit the new conditions imposed by the removal of the eye. The greatly increased size of the supraorbital is notable. The sclerotic bones, not illustrated, are normal and ossified in the river fish but they degenerate and disappear along with the globe, except as they are possibly represented by some small cartilaginous remnants. The curious backward extension of the angle of the operculum in the Cueva de los Sabinos fish and its median separation from the operculum were hardly to be expected. The pointed posterior process of the supraoccipital is reduced in size materially in this series, moving forward as it and the parietal usurp the place occupied by the reducing frontal on the top of the skull.

The above-mentioned changes are hard to comprehend and give the impression of being hit-or-miss and that they might just as well have taken on a variety of other arrangements. On analysis it is seen, however, that actually there is a large amount of regularity in these transforming skulls and that the osteological elements are moving and rearranging themselves under the force of some general regulating control. This may be most readily visualized if we make use of the methods of Thompson (1942) in which some system of coordinates is established on the original form and allowed to distort itself as the lines follow the elements that they intersect. In such construction it is a more or less general practice to start with a set of right angled rectilinear coordinates. This pro-

cedure will yield all the usual data from such a series, but in the present case, instead of applying the simple Cartesian system, it was found to be easier to follow the transformations by the use of a system of polar coordinates with its origin at the center of the eye. The reasons for this are manifest. In the generalized fish skull the surface bones are arranged in a series of essentially concentric elements about the eye. This is obvious from Text-figure 1a. This same skull is shown in Text-figure 2a with such a grid of polar coordinates superimposed upon it. These coordinates are purely arbitrary in dimension and any other distances between the lines would have been just as suitable. Following these through to La Cueva Chica blind fish, Text-figure 2b, the regularity of the changing elements in their basic topography is evident and this stage is clearly intermediate between the river fish and the further advanced Cueva de los Sabinos fish, Text-figure 2c. From even a cursory examination it at once becomes evident that the whole skull, as a unit, is shifting and what would at first seem to be capricious changes in bone shapes and sizes are actually mandatory on each element if it is not to do violence to some master plan that controls the architectural changes.

It is curious that the radial ordinates in all still find a common center in the orbit and it is possibly more than accidental that the central circular ordinate becomes more or less bean-shaped, with the concave side uppermost, which is in agreement with the shape that the reduced eye capsule approaches. It should also be noted that it is only by treating the  $so_3$  in its three parts as a unit that the integrity of the regularity of the intersecting coordinates can be retained. This could be taken to suggest that this increase in number is truly due to a process of fragmentation. Likewise in Text-figure 2c, where  $so_3$  is again a single bone, if the other two continued to exist and were treated as before, as a unit, the regularity of the superimposed grid would be destroyed. In a similar manner the other cranial elements could be discussed, as all subscribe to this general proposition. That is, if they were disposed in any other way, independently of the rest, and there is adequate room from such changes, a smooth flowing grid of parallel or regularly diverging lines would not fit. For example, the greatly expanding supraorbital and the contracting frontal would seem to have no independent reason and the two could have remained very much more as they were and still jointly cover the same space, but as is clear from the figures





TEXT-FIG. 2. Transformation of polar coordinates centered in eye. **A.** Normal-eyed river fish. **B.** Fully blind specimen from La Cueva Chica. **C.** Cueva de los Sabinos fish.

they do change their relative sizes, as if merely to meet the inscribed coordinates in a regular manner.

If it is objected that there are actually small divergencies in each of the two distortions of the initial grid it must be borne

in mind that such divergencies can be of two sorts: partly organic irregularities and partly artifacts due either to the difficulties involved in handling these small skulls or to the ineptness of the draughtsman. The remarkable part of the constructions seems to the author to be, not small discrepancies but rather that there is such a large amount of profound agreement between the distorted grids and the skull elements themselves. It must be borne in mind in this connection that similar constructions have been made between related species which had all their organs intact and merely varied in dimension. When, in a case such as the present, a dominating organ is merely subtracted, it would seem to be of more than passing interest that the remaining parts do show such a fundamentally simple basic plan in reconstituting themselves. It also goes far to indicate the nature of the influence of the eye on the whole pattern of development of the fish skull.

In making these constructions the actual method employed was to point off, item by item, the intersections of a given line corresponding to the grid placed on the normal-eyed skull. Then a line was drawn through these points freehand as one might draw such a curve from any biological data. Thus, some of the points fall exactly on the line and others scatter slightly to either side of it. It would have been a greater refinement to use some method of curve fitting such as the method of least squares, but the limitations of accuracy of the basic material clearly do not warrant such elaborate treatment. When these lines were inked in with the aid of draughtsman's curves it was discovered that the radial ordinates, whatever the nature of their curvature, were all clearly not logarithmic, but that the concentric ordinates partook of this character to a very large degree. That is to say, it was found that for the latter the so-called draughtsman's "Logarithmic spiral curve" fitted these freehand curves perfectly for much of their length while for the radials it was necessary to employ the so-called "Irregular or French curves" to obtain a fit.

Those portions of the concentric ordinates anterior to the diagonal passing through the coracoid,  $so_3$  and supraorbital, maintained their logarithmic feature almost completely. Those posterior to this line took on a distortion, increasingly so as they approached the opposite diagonal, passing through the mandible,  $so_2$ ,  $so_5$  and the scale bone. Nevertheless these curves were nearly all drawn by means of the logarithmic spiral.

All this would seem to indicate the very great influence of the eye on the whole architectural plan of the skull. It is interesting to compare this essentially exponential rearrangement of a skull with its central element removed with the logarithmic growth forms of mollusc shells discussed at length by Thompson (1942). The fact that in a structure as complicated as a fish skull such logarithmic elements are clearly present, as have been so simply and elegantly demonstrated in a clam, is evidently due to the fundamental nature of growth, which in an intricate structure becomes involved and complex but does not obliterate the basic regularities inherent in organic development.

If we look upon this polar grid as a field-of-force diagram in which the concentric ordinates represent equipotential lines, the eyed fish would seem to have its elements disposed very much in accordance with the grid centered in the eye as arbitrarily laid down. A notable exception to this is the disposition of the supraoccipital, which has a strong radial trend. In the other two fishes it will be noted that the greatest distortion of these grids is close to, but not identical with, the seemingly radial trend of the supraoccipital. The grids conceived as fields of force change in such a way as to suggest that there is only one pole of any significant magnitude in the area covered by the grids, namely, that centered in the eye. If another were present it would be expected to lead to some dumbbell-like curves, which are clearly absent. On this basis the curious outward extension through the scale bone becomes explainable on the basis that it is due to another field of influence lying outside of the area of the limits of the grid and which if extended might produce such dumbbell-shaped figure characteristic of a bipolar field. The only evident structure that this diagonal and the "points" of the concentric ordinates are directed toward is the base of the dorsal fin, which, in advance, would be expected to exert such an influence. This is not reflected in the original "monopolar" field which is completely arbitrary, but shows good agreement with the circular disposition of the skull elements, except in the supraoccipital area where they appear to be radial in arrangement as previously noted. Clearly, then, when these circles distort with the shifting skull elements, they become affected by any other influence, such as that of a second polar field, which is ignored by the very nature of the original grid. This is actually what has evidently happened in these transformations. It thus may not be far from the truth to say that these

diagrams indicate the almost complete dominance of the eye except as modified by a dorso-caudad influence probably rooted in the dorsal fin.

Considering the concentric circles of Text-figure 2a not as polar coordinates, nor as equipotential lines of force but as simple geometrical figures expressible in formulæ on ordinary graphic treatment, it is possible to express the first by the equation

$$(x-p)^2 + y^2 = e^2x^2$$

This, of course, is the basic formula for conic sections, of which the circle is merely a special case, and which is more simply expressed as

$$\frac{X^2}{M^2} + \frac{Y^2}{m^2} = 1$$

in which  $M = \frac{1}{2}$  the major axis and  $m = \frac{1}{2}$  the minor axis. The other two grids should be expressible by some exponential expansion of this expression. Then the difference between the three expressions should yield a mathematical measure of the basic nature of these differences. Obviously with the present case the labor involved would hardly justify making the involved calculations necessary and this is mentioned merely to indicate an approach that might have considerable utility in other but similar connections.

Lest it be thought that some artifact has been introduced by centering polar coordinates in the eye, that is, on a structure in which the elements are obviously arranged more or less concentrically, other constructions have been made. One on an orthogonal basis shows essentially the same thing, as it necessarily must, but in not so clear a fashion; it consists of both horizontal and vertical ordinates approaching each other in the eye region and suffering considerable distortion in the temporal region; its verticals and horizontals in this region both bend toward the dorsal fin. Another construction on polar coordinates centered in the scale bone shows approach of the concentric ordinates in the eye region while three of the radials, the anterior horizontal, lower vertical and the included diagonal, approach each other in the eye region and pass through the scale bone and with slight angular divergence also point to the dorsal fin region.

Instead of discussing the matter in terms of centers of influence—which was based primarily not on these constructions but on the long recognized concentric arrangements of the surface bones of the head it might be more appropriate to consider the matter in terms of lines of

strain; the large obvious one in this case being that which runs diagonally upward and back from the mandible through the eye and occipital region. Since the skull is under various strains from muscular attachments it is perhaps to be expected that such a distortion line should appear in a direction involving both the powerful mandibular musculature and to the point of attachment of the occipital condyle which involve also the whole locomotor body musculature. Such considerations, however, would carry us beyond the province of this communication.

A still further analysis can be made by these methods for the purpose of trying to understand their full implications. If any sets of the constructions be drawn superimposed on one paper, then the homologous intersecting ordinates may be connected by lines of varying length with an arrow at their forward end indicating direction of travel of this point on the transforming skull. Very complicated diagrams result that do not look unlike weather maps with their arrows of wind direction, but in which the length of the arrow indicates the proportional distance of travel. By combining visually each of the three sets of diagrams, using different ordinates, it becomes apparent that all show the same features in different terms; this agrees nicely with what has already been set forth. But again this is not the place for extended discussions of such matters.

As further evidence of the similarity of these constructions to those of fields of force it may be mentioned that Hartridge (1920) and Ponder (1925a and b) applied the equipotential curves of Cayley, developed to describe magnetic fields, to the shapes of erythrocytes, and Breder (1943a) discussed them in connection with the shapes of fish eggs. With the information at hand, based on the construction of the polar grid, it would be of interest to recalculate the whole matter on a basis not of equally spaced concentric lines but on the locus of the equipotential curves of Cayley; but this would clearly carry us out of the bounds of the present contribution and no further into an understanding of the eye itself.

Obviously, what has been dealt with here is a projection of one of the three dimensions and for a rigorous analysis all should be considered, just as the equipotential curves of Cayley are descriptive of surfaces and not of lines on a plane. Breder (1943a) discusses these relations in connection with fish eggs and Thompson (1942) gives an extended dissertation on the whole matter.

The preceding discussion has centered on

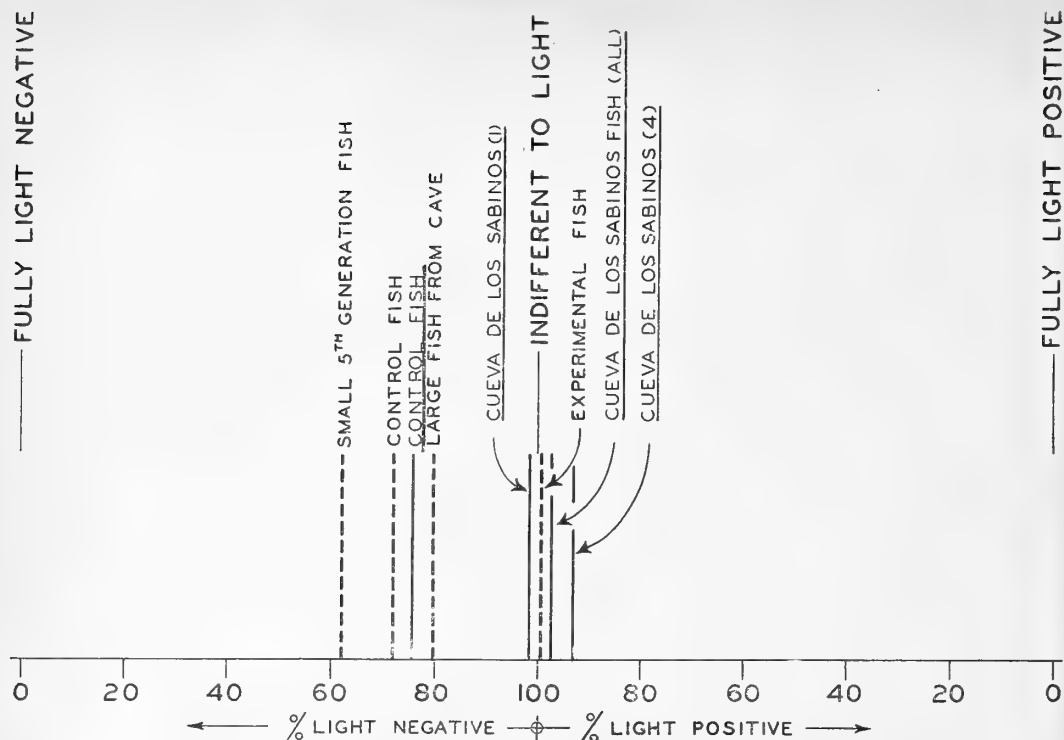
the dermal elements of the skull and suffice to indicate the essential regularity of the modifications. No attempt has been made to analyze the rearrangements of the chondrocranial elements which among other things would practically demand a difficult three-dimensional treatment. It was evident from the sections however, that the bones forming the eye socket underwent extensive modification. These did not close in, as might be thought, but became thinner and lost their solid attachment to the brain case, to some extent actually increasing the tissue-débris-filled eye socket in the Cueva de los Sabinos fish.

#### EXPERIMENTS ON LIGHT REACTIONS.

In order to determine the extent of light sensitivity in the Cueva de los Sabinos fish, an experimental approach was made similar to that employed by Breder & Gresser (1941a and c). For this purpose two troughs were prepared with one end covered and the other under the influence of a 25-watt light. They each measured thirty-nine by seventeen and one-quarter inches and were filled with water to the depth of one and one-half inches. Thus there were two equal compartments each nineteen and one-half by seventeen and one-quarter inches and identical except that one was illuminated and the other under a solid cover one-half inch over the water's surface.

At five-second intervals the positions of the fishes were noted in reference to which compartment they occupied. From this work the data of Table I were compiled and directly compare to the earlier work on the other forms. It is clearly evident from this Table that the fish from Cueva de los Sabinos show no clear reactions to light under the conditions of the experiments, as compared with the earlier studies or as compared with the La Cueva Chica specimen used as a control against the Cueva de los Sabinos material. Because of the agreement of the latter with the more extensive earlier studies, it was possible to reduce the number of tests, as all the earlier work can be considered as a control for the present experiments.

Text-figure 3 shows these results in graphic fashion and compares the present data with that of the earlier work. This is indicated by dotted lines. It will be seen that the present control fish, La Cueva Chica stock, gave readings of between 60 and 80 per cent. light negativity in terms of random expectation. As pointed out by Breder & Gresser (1941a), the smaller of these approach 60 per cent. of expectation while the largest approach 80



TEXT-FIG. 3. Comparison between light reactions in fishes from La Cueva Chica and from Cueva de los Sabinos, shown by solid lines, and between La Cueva Chica specimens with and without optic capsule, shown by dotted lines, from Breder & Gresser (1941b). New data indicated by underlining. All expressed in terms of expectancy of random movement. See text for full explanation.

per cent., the reason clearly being due to the greater absolute mass of tissue overlying the blind but light-sensitive capsule. Its removal, as they showed, places the fish close to 100 per cent. of expectation, as indicated in Text-figure 3. It is close to this point that all the readings on the Cueva de los Sabinos material is located. This was, of course, to be expected since it has been shown that these fish lack all remnants of retinal structure and there is no connecting optic nerve. They are thus normally comparable to the condition produced in the La Cueva Chica material by operation.

The La Cueva Chica stock is thus separated from that from Cueva de los Sabinos as well as from operates by a range of nearly 20 per cent. as measured by this system of notation, checking perfectly with what might be deduced from the morphology of the situation.

#### DISCUSSION.

Although in all the experiments on light reactions in this and the two earlier papers care was exercised to avoid thermal differ-

ences in the light and dark chamber, the direct effects of radiant energy of course could not be eliminated. Although all examples with some light sensitivity reacted negatively to light, see Breder & Gresser (1941a and b), it will be noted that those forms without an optic nerve or with the capsule removed show a mean value slightly on the positive side. Since in all there have been 72 such experiments made, the present data and that of Breder & Gresser (1941b), this may well indicate a significant difference. Expressed another way, all but one of the sets of experiments were somewhat over 100 per cent. on the scale adopted. It is suggested that this may be reflecting a slight positive bias on the part of these apparently light-indifferent fish to accept the warmth of the radiant heat of the light bulb, perhaps very much as a blind man can detect the edge of a shadow if the sun is bright, but on a much finer scale of discrimination. Since these fish move readily into the direction of warmth, as has been indicated before, this effect is surely to be expected. To measure this in any great degree of refinement a

number of difficult obstacles present themselves and the present methods are not delicate enough to certainly determine it. Such an attempt has not been made, for with other facts already at hand it seems to be not of sufficient significance in present connections.

Scharrer (1928) has shown that blinded *Phoxinus laevis* are light sensitive. This sensitivity he found located directly in the midbrain, made possible, at least, by the thin and not completely opaque overlying structures. He concluded that possible skin sensitivity was definitely not involved. It might be that the effect above considered is actually a measure of a similar condition in these fishes. Experiments along the line of those conducted by Scharrer would have to be undertaken in order to determine these effects, although it does not seem that he eliminated the possible effect of radiant heat, as above considered, from his experiments.

In connection with this it should be noted that very few fishes have been unequivocally shown to possess integumentary photosensitivity. It is evidently present in (*Chologaster*) *Forbesella*, Eigenmann (1909), and in *Amblyopsis spelaeus* DeKay, Eigenmann (1909), Parker (1909a) and Payne (1907). In addition to these fishes proper it is present in larval *Petromyzon* (or *Lethenteron*) Parker (1909a). Although absent in *Amphioxus*, photosensitive cells are located in the nerve tube and exposed by the transparency of the creature, Boeke (1902) and Parker (1908a and b).

A variety of species, *Fundulus heteroclitus* (Linnaeus), Long (1904), Parker (1909a and b), *Fundulus majalis* (Walbaum), Long (1904), *Mustelus canis* (Mitchill), *Anguilla rostrata* (LeSueur), *Stenotomus chrysops* (Linnaeus), *Tautoglabrus adspersus* (Walbaum), *Tautoga onitis* (Linnaeus), *Chilomycterus schoepfi* (Walbaum), *Opsanus tau* (Linnaeus) and *Microgadus tomcod* (Walbaum), Parker (1909b) were shown to have no such sensitivity. It would thus seem that dermal photosensitivity is largely absent in fishes, only the Amblyopsidae having had such demonstrated. Other kinds of such sensitivity, as in *Phoxinus*, would seem to be incidental to the translucency of structures overlying the central nervous system.

Although the La Cueva Chica material will avoid light except if it is overridden by sufficiently large thermal or other differences, it is evident that the Cueva de los Sabinos fish indicate no such negative reactions to light. Thus it follows that while the first are probably held in their cave by this means, the latter are not pro-

tected from blundering into a surely fatal environment by any such mechanism. Until much more is known about the geography of Cueva de los Sabinos we can only speculate as to whether these fish are prevented from entering outside waters by physical barriers or whether there is a continual drain off of that population. Although direct tests have not been made it is to be expected that the fish from Cueva de los Sabinos will be found to react to current and water temperature in a manner essentially identical with those of the fishes from La Cueva Chica and eyed river fish. The essential similarity of their gross reactions as well as minor differences in behavior in reference to other senses are discussed by Breder & Rasquin (1943).

It is possible that physiological methods of greater refinement could show light sensitivity on a "micrometric" basis by some modification of the methods of Kurodo (1932), who showed by a kymograph trace that certain fishes gave an immediate respiratory response to various chemical stimulæ. Such a method was found inadequate to the peculiarities of these fishes as is reported by Breder & Rasquin (1943).

As with the development of chemical sensory changes discussed by the above, the eye structure, the skull architecture and behavior of the Cueva de los Sabinos stock as reported here also suggest that these fish are a further development of the conditions found in La Cueva Chica material rather than that the two are independent developments. Whether or not the present La Cueva Chica material should be looked upon as "hybrids" between some small and isolated group of Cueva de los Sabinos fish and the Rio Tampaon stock made possible by a new contact the present studies do little to illuminate.

Hatch (1941) considers that degeneration occurs in caves, because in the absence of selection, mutations of various kinds can survive and that degeneration follows because most mutations are those of loss. Walls (1942) holds similar views, writing as follows:

"Just how the eyes of any blind fish species were led to disappear, we cannot say. An old idea was that where the eye had become useless, there was a positive incentive for eliminating the organ, since this would save energy both in adulthood and—especially—during growth. This notion seems ridiculous nowadays, for the proportion of a growing animal's food-intake which goes to enlarge the eye is negligible. Most of the energy released from food goes for motor and secretory activity, and only a very small part of the food is converted into new protoplasm. Nor does the disap-

pearance of an eye leave a hole in the head—its volume is occupied by tissues (mainly muscle) which consume just as much energy as the eye had done.

"Though a normal eye is excess baggage to a cavernicolous or limicolous fish, there appears to be no urgent reason why he should get rid of it. Useless organs do not always promptly disappear simply because they have become useless—as witness the human appendix, coccyx, platysma, tonsils, wisdom teeth, *et al.* We are left to suppose that in the immediate outside ancestors of most cave species the eye was 'trying' to disappear anyway, but was prevented from doing so, by natural selection, because it was useful and necessary. The usefulness once removed by the assumption of cavernicolous life, the inherent tendency for the eye to shrink was allowed to express itself, even onto the logical end-result—complete loss.

"This explanation does not tax the imagination of ichthyologists as severely as one might think. In many open-water fish species, reduced-eyed individuals appear as soon as the food supply is made abundant and predatory enemies are removed. Lack of competition then permits the full development of individuals which, since their germ-plasm has undergone 'mutations of loss,' would formerly have been suppressed by starvation or capture. Loss-mutations are known particularly to affect the more complex organs of vertebrates, such as the eye. A species or family in which such mutations occur with especial frequency has of course no advantage, over others, in any attempt to become adjusted to a habitat in which illumination is reduced or absent. But if a group which throws loss-mutations also produces an unusual number of other trial-and-error modifications (as seems likely), then such a group might readily evolve the dermal sense organs, barbels or what-not required to cope with a dim-light environment. Once adapted to dim-light existence, such a group would actually be better off in a cave, if it happened to find one, than outside where there were predators to be dodged. And once inside the cave for good, a rapidly-mutating species would inevitably lose what remained of its eyes, though without being under any positive necessity of doing so."

Pike (1943a and b) would refer such degeneration to thermodynamic irreversibility and states his interesting views as follows:

"Confusion has arisen concerning certain processes which have been called reversible, in living organisms. For four decades, biologists have searched for so-called reversible processes comparable to the so-

called reversible processes of general chemistry. The object was to disprove the existence of supposed vital characteristics of living organisms. A number of these processes have been found, although there has been scepticism concerning their actual reversibility under biological conditions. In these four decades, we have come to recognize more clearly that, in inorganic nature, processes which are not strictly mechanical are irreversible, thermodynamically.

"Two costs must be reckoned in non-mechanical processes—that in free energy, and that in entropy. Unless both can be kept at zero when the operation is put through in the reverse direction, the process is irreversible thermodynamically. 'If an irreversible process can occur, it will occur.' (Houstoun). Unless there is some mysterious mechanism in living organisms to forbid irreversible processes, they will occur. Experimentally, we have found many such, but we have never found one which is reversible thermodynamically. To show the existence of reversible processes in living organisms would be the equivalent to a demonstration of vitalism.

"These considerations bear on certain hypotheses of heredity, the transmissibility of the effects of the environment, and the degeneration of specialized tissues in changed environments, some of which hypotheses postulate thermodynamically reversible reactions, or their equivalent in thermodynamic efficiency.

"It has been asserted that degeneration of eyes of cave forms is due (1) solely to chromosomal changes, and (2) to inheritance of the effects of the environment. Since photo-receptors appear only in species which have some time lived in the light, it seems permissible to assume some causal relationship between light and photoreceptors until demonstration of their complete independence.

"The chromosomal hypothesis of degeneration of the eyes of cave forms postulates that the process of heredity will go on for generation after generation, with no dissipation of free energy or gain in entropy, and, hence, be a truly thermodynamically reversible process, or a process of equivalent thermodynamic efficiency, such as is found nowhere else in nature.

"Since darkness is merely the absence of light, and cannot be a form of energy, it can have no positive effect, and can produce nothing. Since it has no positive effect, the effect of darkness could not be transmitted hereditarily.

"The observed result of living in perpetual darkness is what we would expect when organisms experience a failure of the



driving force concerned with the development of photoreceptors.

"When the phenomena of recession and degeneration, of use and disuse, in ontogeny and in phylogeny, are regarded from the dynamical point of view, there appears to be some fundamental relationship to their irreversibility, in the thermodynamic sense of irreversibility."

There is clearly no basic conflict between these two views or the view that genes carrying eye defects can be perpetuated in such environments and spread through the population by some such means as expressed by Hubbs (1938) of which Breder (1943b) wrote, "An interesting speculation on the possible mathematics of the genetic reduction of other than blind white forms coupled with repeated separation of small population groups is discussed by Hubbs."

In this connection the interesting report of Ogneff (1911) showed that gold fish kept in darkness up to three years suffered histological degeneration of the retina. He was satisfied that his fish were blind. Unfortunately he says nothing about light sensitivity. The eyed specimens from La Cueva Chica were mentioned by Breder (1943c) as follows: "All fish brought freshly from the cave act like the blind fish in regard to feeding. This has been checked twice, all forms from the cave performing circling movements for food finding for at least a couple of months and then those with structurally good eyes apparently learning the meaning of a retinal image and taking on the feeding habits of the river fish. These forms at all times, from the first, 'jump' at the passage of a shadow, like those with merely an exposed retina." It is proposed to check this material histologically to determine if this inability to find food by visual means had to do with retinal degeneration and later reorganization under the influence of light or on a basis of learning. The work of Ogneff (1911) strongly suggests that the former may be playing a large part in this connection. The nature of such changes in either direction should yield data bearing on the views of Pike (1943a and b).

SUMMARY.

- 1. The blind characins from Cueva de los Sabinos, San Luis Potosi, Mexico, differ from those of La Cueva Chica, which is about fifteen miles distant, in that the former show a still further structural loss in eye architecture.
- 2. Nothing is left of the retinal tissue and all that can be found in the socket is a much reduced pigmented cyst which may represent the last of the coroid.
- 3. The last vestige of a connecting optic nerve is gone.

- 4. Along with the eye loss has come modification of the skull, involving a closing in of the circumorbital series of bones, and some de-ossification.
- 5. Great regularity is shown in the rearrangement of the bones of skull with the subtraction of the eye, clearly indicating a reconstitution of the skull as a whole in which the separate elements are without independent action.
- 6. Experiments with a gradient trough show that these fish are fully indifferent to light as compared with the negative reactions of La Cueva Chica specimens.
- 7. Current views on the biology of such degenerative changes are discussed.

TABLE I. TABULATIONS OF EXPERIMENTS ON LIGHT SENSITIVITY.

Each experiment represents 100 notations at 5-second intervals.

Exp. no.	Type of fish	Number of fish	Observed in light	% of random expectation
1	La Cueva Chica <sup>1</sup>	1	30	60
2	" "	1	24	48
3	" "	1	28	56
4	" "	1	63	126
5	" "	1	27	54
6	" "	1	77	154
7	" "	1	12	24
8	" "	1	49	94
9	" "	1	53	106
10	" "	1	17	34
		Mean	37.8	75.6
11	Cueva de los Sabinos <sup>2</sup>	1	49	98
12	" "	1	63	126
13	" "	1	51	102
14	" "	1	45	90
15	" "	1	80	160
16	" "	1	44	88
17	" "	1	16	32
18	" "	1	17	34
19	" "	1	36	72
20	" "	1	89	178
		Mean	49	98
21	Cueva de los Sabinos <sup>3</sup>	4	158	79
22	" "	4	156	78
23	" "	4	226	113
24	" "	4	223	111.5
25	" "	4	240	120
26	" "	4	257	128.5
27	" "	4	273	136.5
28	" "	4	233	116.5
29	" "	4	212	106
30	" "	4	161	80.6
		Mean	213.9	106.9+
		Mean of Exps. 11 to 30		102.5—

<sup>1</sup>This fish seventh generation of tank-reared stock, 49 mm. in standard length.  
<sup>2</sup>This fish from Cueva de los Sabinos, 46 mm. in standard length.  
<sup>3</sup>These fish from Cueva de los Sabinos, between 46 and 49 mm. in standard length.

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**EXPLANATION OF THE PLATE.****PLATE I.**

Sections through the left orbit of specimen from Cueva de los Sabinos.

FIG. 1. The central body represents the cartilaginous capsule within which is a pigmented cyst surrounded by loose connective tissue. Magnification 80  $\times$ .

FIG. 2. A slightly more posterior section showing the medial wall of the capsule to be here composed of connective tissue. At about the center of the connective tissue portion is a mass made up of muscle and possibly an atrophic nerve. Magnification 62  $\times$ .

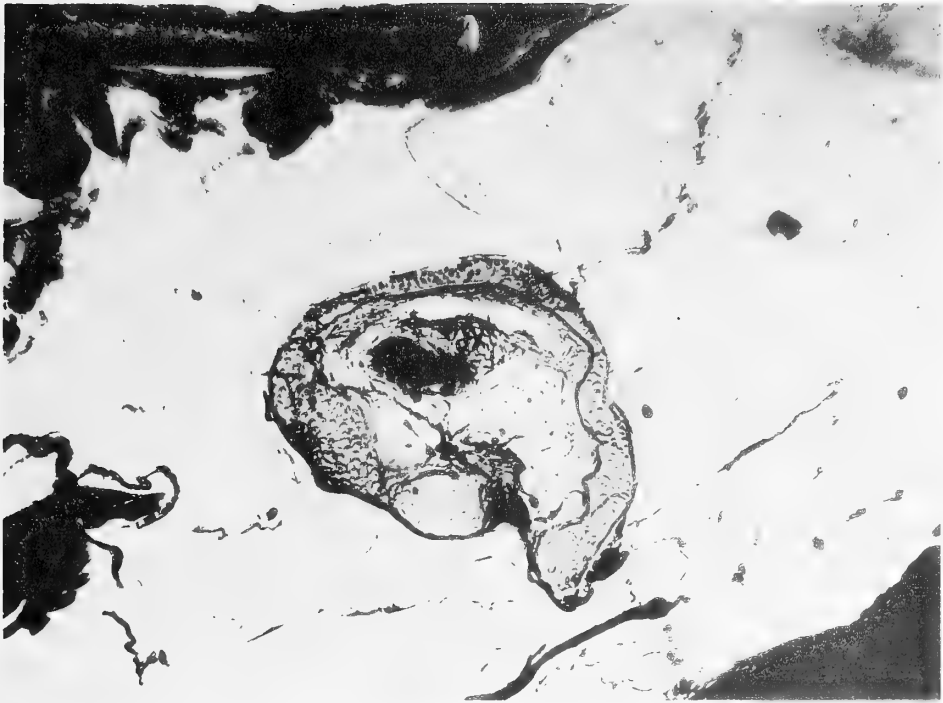


FIG. 1.

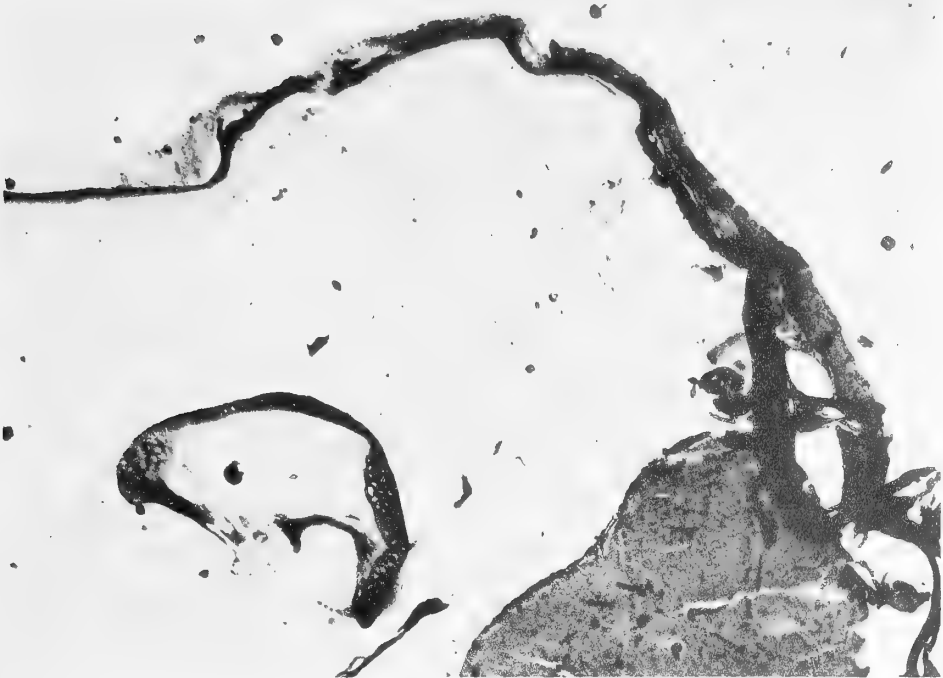


FIG. 2.

OCULAR ANATOMY AND LIGHT SENSITIVITY STUDIES ON THE BLIND FISH FROM  
CUEVA DE LOS SABINOS, MEXICO.



## 14.

Field Notes on the Lizards  
of Kartabo, British Guiana, and Caripito, Venezuela.  
Part 1. Gekkonidae.<sup>1</sup>

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(Plates I-VI; Text-figures 1-6).

[This contribution is a result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana and to Venezuela, all made under the direction of Dr. William Beebe. The Guiana expeditions were made during the years 1909, 1916, 1917, 1919, 1920, 1921, 1922, 1924 and 1926, and the Venezuelan trips in 1908 and 1942. The latter was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

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INTRODUCTION.

In the year 1909, and from 1916 to 1926, eight expeditions went out from this department to British Guiana, and in 1908 and again in 1942 field work was carried on in Venezuela.

Throughout the course of these expeditions many field notes, color plates and photographs were made of tropical vertebrates, and the object of this present series of papers is to assemble and publish these notes and illustrative material. Any change or alteration of the original notes is placed between brackets. The chief value of these data is that they are concerned with living or recently killed specimens.

The observations in Guiana were made in one-quarter of a square mile of jungle at Kartabo, and those in Venezuela at or close to Caripito, which is only 528 kilometers northwest of Kartabo.

In addition to numerous technical papers in *Zoologica* and several popular volumes, there have been published the following general ecological summaries: *Zoologica*: (Kartabo) Vol. II, No. 7, 1919, pp. 205-227; Vol. VI, No. 1, 1925, pp. 1-193; (Caripito) Vol. XXVIII, No. 9, 1943, pp. 53-59. Also see "Tropical Wild Life In British Guiana" by Beebe, Hartley and Howes, published by the New York Zoological Society, 1917, pp. 1-504.

My hearty thanks go to Dr. Charles M. Bogert of the American Museum of Natural History and Dr. Karl P. Schmidt of the Chicago Natural History Museum for identification and for bringing up to date my out-worn names of many years ago.

My original field numbers and other data have been appended to descriptions, breeding and other notes. These specimens are either in the collections of the Department of Tropical Research or in those of the American Museum. In the latter case the original field numbers are still attached, with the additional catalogue numbers of the Museum. Whenever the term total length is used, a perfect, unregenerated tail is understood. Most of the figures in the plates are black and white reproductions of original color paintings, so only the pattern is preserved. The following are from photographs of living specimens taken in the jungle: Pl. II, Fig. 4; Pl. IV, Figs. 9, 10; Pl. V, Fig. 14; Pl. VI, Fig. 16.

FAMILY *Gekkonidae*.

Eleven species of geckos were found at the two localities of study, Kartabo and Caripito, ten at the former and three at the latter. Only one of the Venezuelan species was absent from Kartabo. One of the

<sup>1</sup> Contribution No. 694, Department of Tropical Research, New York Zoological Society.

latest check-lists of South American lizards (Burt & Burt, 1933) records nine species of this family from northeast South America, of which we found every one in our restricted areas. In addition we studied two others at Kartabo, one of which (*Gonatodes humeralis*) was previously recorded only from the basin of the Upper Amazon, and the other (*G. caudiscutatus*) from Colombia and Ecuador.

Some species of this family of small, very primitive lizards are familiar to every visitor to the tropics. They are not uncommon, they usually are provided with voices, and several are almost certain to be found in houses and camps situated near woods or jungle. Although perfectly harmless these geckos are universally feared by the natives, who call them by such names as Fathers of Leprosy and Poison Shooters. Most are nocturnal and are without movable lids to the eyes, and furnished with vacuums of sorts on the soles of the feet, enabling them to cling to and run over smooth vertical surfaces.

Geckos breed for the most part in the long rainy season and the eggs, one or two in number, are deposited in mould or the dust of decayed logs and other suitable places in the jungle.

Patient study of the habits of geckos might very probably yield interesting results for they are very primitive even for reptiles. No fossil forms of the family have been found but the remains of closely related lizards are known from the early Mesozoic, and we know that more than one hundred million years ago their tails were being shed as a means of safety first. Even today, geckos carry around with them such indelible proofs of their primitiveness as amphicoelous vertebrae, the presence of intercentra and an occasional well-developed second branchial arch.

***Gonatodes albogularis*** (Dumeril and Bibron, 1836).

**Names:** Stripe-shouldered Gecko; Black-and-white-tailed Gecko.

**Range:** Northeastern South America and the Dutch Leeward Islands.

**General Account:** In Caripito, both in abundance, in habits and in superficial appearance, this little gecko takes the place of *G. annularis* as we had found the latter at Kartabo, 528 kilometers to the southeast, south of the Orinoco. In notes on a collection of lizards from Surinam, Van Lidth de Jeude lists "Three specimens [of *albogularis*] with coloration of upper parts resembling closely those of *G. annularis*." I found, however, no record of *G. albogularis* either in the Georgetown Museum or in my eight years in the field in British Guiana.

My field name for temporary use was "stripe-shouldered" as compared with "spot-shouldered" for the other species and suggests one good distinction, this very characteristic marking being in *albogularis* in life rather a large, irregular blotch of brown or black with a vivid white streak across the middle, than the round black ocellus, more or less bounded with lighter color. The fully developed males usually possess some dorsal red, and the markings of the back and tail recall the very pronounced pattern of the females and young of *annularis*. All the dorsal markings, especially the terminal black and white caudal bands, are emphasized in newly hatched individuals. (Pl. I, Figs. 1 and 2).

Many of these lizards were taken in our pits, showing that they were active on the ground at night. The majority thus captured were in Pit 13, which was the only one actually in open savanna, about thirty feet from low second growth. No other species was found in this particular pit, but for several weeks stripe-shouldered geckos fell in by ones and twos. When two were found at once, they were, except in one instance, both males or both females, emphasizing the solitary or at least unpaired habits of these lizards. An unusually large number were in Pit 13 in early April, several weeks before the rainy season began. Three individuals lived in the laboratory, visible mostly at night high up on the walls.

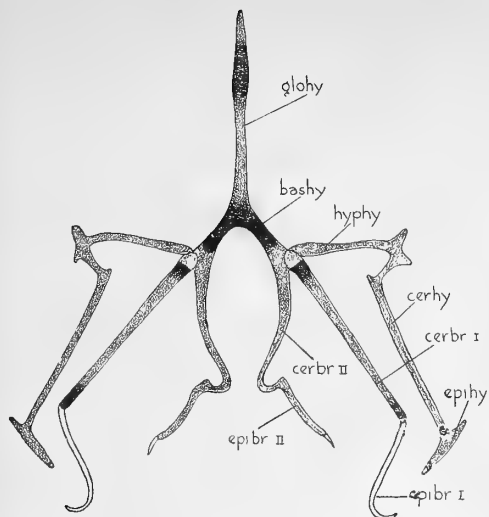
Male, not breeding, body length 30 mm., total length 66 mm. (No. 30,043, Caripito, April 11, 1942, Color Plate 1538):

**Color in Life:** Upper parts grayish-brown, with paler gray lines on the head and a wide vertebral band to beyond the base of the tail. A dark brown humeral blotch bisected by an irregularly crescentic, transverse band of pure white, almost meeting on the mid-back. Back and limbs marbled with shades of brown and freckled with white. At the posterior insertion of the hind limbs is a small paired imitation of the humeral marking, small jet black spots flanked posteriorly with white. These are repeated six times down the tail, spreading out posteriorly into broad, black and white bands.

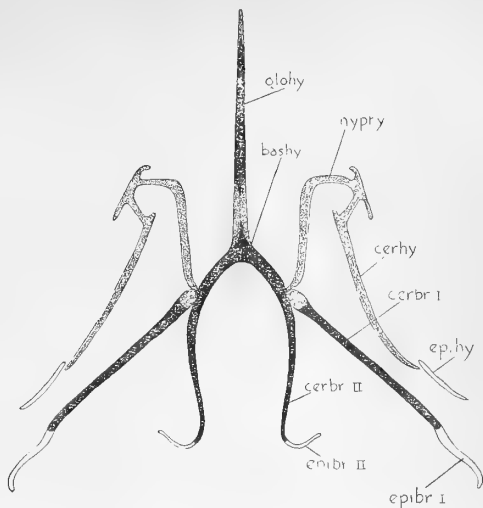
Lower labials dull lemon, chin and throat bright lemon yellow, fading posteriorly into yellowish-gray. On the chin are three large spots of rich orange, and behind these, three converging bands of the same color, freckled with brown. Iris mottled with two shades of brown.

Breeding male, body 36 mm. (No. 30,100, Caripito, Pit 4, May 14, 1942):

**Color in Life:** Dark brown; tip of snout white; faint patch on occiput; white line at insertion of fore limb, extending up and



TEXT-FIG. 1. *Gonatodes albogularis*. Hyoid of 24-hours-old lizard.  $\times 15$ .



TEXT-FIG. 2. *Gonatodes albogularis*. Hyoid of adult, breeding female.  $\times 11$ .

obliquely back, almost meeting its fellow at mid-back. Lores reddish. Indian red line around antero-inferior circumference of eye; a broad red line back from eye below white stripe; another red line on side neck back to shoulder stripe; a few indistinct red spots on body. Below cold gray.

Breeding female, body 35 mm., total length 75 mm. (No. 30,093, Caripito, Pit 4, May 6, 1942):

*Color in Life*: Pale brown on head, back and limbs. A very wide dark brown band from ear to half down tail each side of the body. the upper side of this band is zig-zag, cutting into the dorsal light ground color with a series of angled points. Legs mottled brown. In front of the shoulder is a large white blotch, surrounded by a wide light area, and this in turn by a black band, all these frames being open in front toward the head. Chin and throat dead white, sparsely dotted with dark, with a series of larger spots along the sides. Lower body and tail warm orange.

On the posterior half of the tail, the brown of the body gradually changes to rings, which form the proximal boundary of a series of pale brown bands. On the under side of the tail these light bands become brilliant white. The reason for this is apparent when I watched this individual lizard frightened. The tail curled far up and forwards over the back, forming a conspicuous, banded black-and-white banner. An enemy would certainly snatch first at this bright colored moving structure, and the tail then breaking off and beginning its frantic, isolation dance, the owner would escape. In the oviduct was a large, soft-shelled egg nearly ready for deposition.

*Hyoid*: Newly hatched, 24 hours old, (Text-fig. 1), No. 30,018, total length 30 mm. (KOH No. 2,500, Caripito, March 1, 1944). Glossohyal long and slender (1.7 mm.). It is hyaline except for one-quarter of its length beginning near the tip, this area showing considerable calcification. The clarity of the glossohyal continues to the division into the basihyals, all of which elements show solid calcification. At the lower part of this area is a distinct shoulder or socket from which spring the first two gill arches. The hypohyal arises from the upper rim of the shoulder, extending *horizontally* as an almost straight element, slightly larger in caliber at the base, and expanding distally into two, widely separated points. From the lower point a short, obliquely backward directed rod is seen, from which there arises the ceratohyal. So firmly is this pair of bones attached to the auditory apparatus that in dissection, both were torn away from their hypohyal attachment, remaining firmly fixed to the otic area of the skull. This extremity shows a solidified, large, flat, diaphragm-like expansion.

From the hypohyal socket itself arises the first ceratobranchial (1.7 mm.), the junction being by an enlarged, rounded, hyaline head, with considerable calcification immediately behind it, suggesting a hint of separateness which might justify considering it a hypobranchial relic. The distal extremity which is slightly calcified, gives rise to a slender epibranchial curved into a hook at the end. Although the hypohyal calcification ends abruptly at the socket, the arch extends posteriorly with no change in curvature and only a slow narrowing, as the sec-

ond ceratobranchials. These are elaborately developed and end in elongated, angular extremities, and at the very tips there is a minute, clawlike bit of cartilage, probably a vestigial second epibranchial. This entire third arch is quite devoid of calcification.

Adult breeding female, (Text-fig. 2), No. 30,093, total length 75 mm. (KOH No. 2501, Caripito, May 6, 1942). The hyoid of this adult female is actually only 32 per cent. or one-third larger than that of the day old specimen, and in eyeball diameter there is even less difference, an increase in the adult of only one-fourth or 25 per cent. Opposed to these organs so valuable to the newly hatched young lizard, are the relatively less important total lengths of young and adult, 30 and 75 mm., respectively, an increase of two and one-half times, or 250 per cent.

The hyoid of the adult gecko differs from that of the twenty-four-hour lizard in only a few important ways. The glossohyal is relatively longer and more slender, and the outward curve of the hypohyals is somewhat more pronounced. In my description of the juvenile hyoid I purposely italicized the *horizontal* position of the hypohyals, as being radically unlike that in the normal hyoid arch of adult geckos. In the present specimen these elements have swung forward quite 90 degrees into the specialized gekkonid position. This forward shift includes the entire hyoid arch, and seems to have brought about or perhaps may be said to have been the result of a loss of direct connection with the auditory apparatus, so that the end of the ceratohyal is well anterior to the end of the first ceratobranchial, and the extreme distal tip instead of being closely united to the diaphragm-like transverse element, dies out, and shows now, instead, a short separate bit of cartilage lying alongside its tip.

The first branchial arch shows little change except a shortening of the epibranchial, and the same is true of the terminal, irregular filaments of the second ceratobranchial.

**Breeding:** On March 1, 1942, at Caripito a gecko hatched from one of six eggs deposited under the bark of a rotten log by three or more females of this species. The eggs measured 6 by 7.5 mm., the newly hatched lizard 30 mm. over all. The color in life was dark brown with a series of orange-edged black spots down each side of the back. The tail ended in conspicuous bands, two white and two black. The tail was held high in the air from the first step after hatching, and waved from side to side when walking. March 2nd the lizard had shed and eaten its skin. From this night on, the change from dark brown to very pale body and intense black-and-white-banded tail

was very marked. A second egg contained an embryo only three-fourths developed, very lively but hampered by a considerable amount of yolk. Its most conspicuous markings were the shoulder stripes. It was 28 mm. over all, and the tail was very active. The other eggs were almost fresh, so that the entire six must have represented a communal laying on the part of several females.

***Gonatodes annularis* Boulenger, 1887.**

**Names:** Spot-shouldered Gecko, Yellow-throated Gecko; Wood Slave (Guiana Creole); A-tah-zick (Akawai Indian).

**Range:** The Guianas.

**General Account:** This is the most abundant of the small species of geckos at Kartabo. Its favorite haunts are old stumps, hollow and fallen trees and the débris behind half-rotten leaf spathes of palms. I once found two at a height of thirty feet in a bromeliad. They were seen now and then in the laboratory but were not as conspicuous as *Sphaerodactylus*, nor as skilful in climbing vertical surfaces. They are less nocturnal than *Thecadactylus* and *Sphaerodactylus* although, like the latter, they have round pupils. They are active on cloudy days but I never saw them in bright sunlight.

The food of this species consists of small insects, especially termites, as well as collembolas, diptera and ants. A pet monkey caught and ate one without much zest, and repeated this on three occasions. The only other observed enemy was a large marine toad which devoured two, and a young trumpet which killed but did not eat a spot-shouldered gecko which escaped from a vivarium.

These geckos are decidedly solitary and I never found a pair close together, but in three cases (twice in the vicinity of eggs) a male and a female were present in the same log. Twice I found a female actually touching the eggs, one and four eggs respectively. While only a single egg is deposited at a time, I am reasonably certain that as many as four may be laid at considerable intervals in the same cavity by the same individual. Eggs are always hidden beneath soft, fine débris well below the surface. When the female was found with the eggs, she too, was buried out of sight in the damp sawdust. Four-fifths of the eggs found were laid during the long wet season from April to September. One egg, kept under natural conditions, hatched after 52 days from the time of discovery, apparently indicating this remarkable length of time as a minimum period of development.

In one case I found two eggs buried in a termite nest, and a newly hatched dead lizard, showing that unlike tegus (*Tupinam-*



bis) in corresponding conditions, these weak geckos cannot free themselves when built in.

Whether the throat in this species of gecko is immaculate or distinctly lined is a character quite independent of age or sex, but in the adult male it seems invariably yellow. In sexually active males there is always a large amount of red on the dorsal surfaces. The dorsal irregular spotting or banding (see figure of coloration of type, *Proc. Zool. Soc. London*, 1887, p. 153) is often apparent in adult females and in the very young of both sexes. In five such individuals, females and young, very distinctly marked in life, not a trace remains in the preserved specimens.

Male adult (No. 189, Kartabo, June 27, 1919):

*Measurements*: Length 68 mm., head 9, tail 34 (renewed portion 31), eye diameter 1.7, snout 4, eye to ear 3.2, fore limb 11, hind limb 16 mm., weight 1 gram.

*Color in Life*: Head in general greenish-yellow, the lip scales all around above and below reed yellow (colors from Ridgeway's nomenclature), face markings olive yellow. (Pl. I, Fig. 3). These latter include a snout spot, an irregular line in front and another behind the eye, the head below the eye and back to and including the ear, and a small spot well above the ear. Dorsal body surface violet gray thickly granulated with Brazil red back to mid-body, where the red concentrates and forms two dorsal and two lateral lines of three to five large round spots. In front of the insertion of the fore limb is a large ocellus, black, banded with smoky, and with a wide vertical line in front and another behind of yellowish-white. Tail amber (broken off twice near base and grown completely again). Limbs tawny olive, the scales tipped with black. Chin, throat and lower neck bright olive ochre. Ventral body, upper arm and leg olive buff, tail from just beyond vent vinaceous fawn.

*Scalation*: The ventral scales are flat, well separated and with numerous fine black dots. A large area, rounded, abruptly marked on the posterior belly at equal distances from the vent and the insertion of the thighs, and an elongated area on the under side of each thigh, consists of specialized scales, much swollen and immaculate. Those on the thigh number about eight long and three or four scales wide. The ventral scalation of the renewed tail is very irregular, three or four transverse scales extending clear across, being followed by a broken irregular series of small scales, then more transverse scales.

Male adult, length 71 mm., tail 36, weight 1 gram (No. 782, Kartabo, May 17, 1922):

*Color in Life*: General color dark brown,

head variegated with red and green. Dark shoulder spot bordered behind by white line. Two light brown spots at base of tail above. Chin and throat and under parts greenish-yellow.

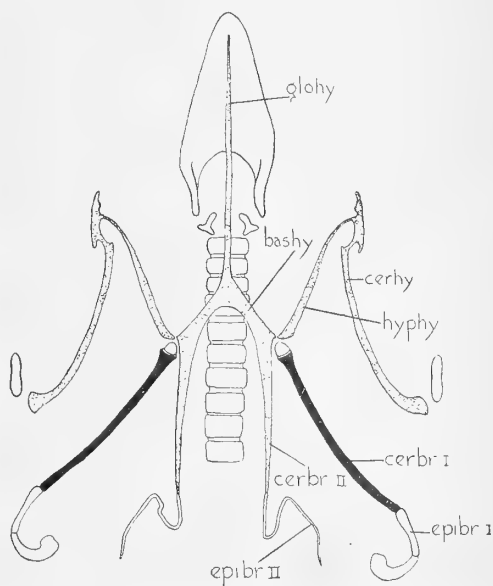
Female breeding (No. 558, Kartabo, August 9, 1922):

*Measurements*: Length 75 mm., head 11, eye 2, fore limb 10, hind limb 12, tail 41.5, weight 1.1 gram. Egg about to be laid.

Male adult, length 83 mm. (No. 531, Kartabo, March 8, 1922, Color Plate 330):

*Color in Life*: Head and back dark olive green with broad, rather irregular bands of carmine. The lores are wholly carmine, and three lines extend back from the eye, the lowermost curving up over the humeral ocellus. Labials and all four limbs light olive green. Chin and throat immaculate, apricot yellow. There is a large, roundish black spot on the shoulder with a slightly angular, very conspicuous broad white line extending transversely from the lower insertion of the fore limbs almost to the mid-back. In the same individual, preserved, only the black spot remains with all the red gone and the white line as an obscure gray shade. Otherwise the lizard is monochrome dull brown.

*Hyoid*: Male adult, length 65 mm. (KOH No. 2018, Kartabo, June 24, 1920. (Text fig. 3). Description and drawing checked with identical hyoid of No. 2020, same length and sex): Glossohyal or lingual process a slender, needle-like rod 3.5 mm. in length to the base of the forked but otherwise undifferentiated basihyals. The anterior 1.7 mm. of the glossohyal is covered with a broad, spear-shaped tongue core, 1.5 mm. wide



TEXT-FIG. 3. *Gonatodes annularis*. Hyoid.  $\times 10$ .

with two transparent posterior cornua. From their point of divergence, to the shoulder articulating with the arches, the basi-hyals measure 1.3 mm. The proximal element of the hyoid arch, the hypohyal, is represented by a slender rod of 2 mm. extending obliquely forward from the basihyal, curving slightly outward for the distal half millimeter, and connecting by a close-fitting joint with a curious, skate-shaped affair. From the inner side of this, two-thirds towards the rear, arises the long, slender, backwardly curved ceratohyal 2.8 mm., enlarging slightly but evenly throughout its length, and ending in a truncate, wide-flanged tip close to the ventral aspect of the auditory apparatus. The articulation of the first ceratobranchial shows a distinct, strongly marked, curved head, the remains of the hypobranchial. The ceratobranchial itself follows the general direction and length of the ceratohyal, but is slightly longer. The end of this part of the hyoid apparatus is strongly curved and distinctly divided into two distal segments, which may represent the epibranchial and perhaps the pharyngobranchial elements of the first branchial arch.

A third arch is well developed in this primitive little lizard. These second ceratobranchials extend back as two strong spines from the articular area of the basihyals, completing with them a general wishbone shape. From the end of each depends a long, delicate, thread-like strand of tissue, of perhaps degenerate epibranchial origin.

A cleared hyoid of *Gonatodes caudiscutatus* is identical with the above, except for a reduction in the size of the tongue core.

**Breeding:** On August 23, 1919, an egg of this gecko was found in a broken palm stub close to the laboratory at Kartabo. An adult female lizard was a foot away and was accidentally killed when captured. The egg must have been deposited some time before, as it hatched the same day.

I watched the lizard (Cat. No. 229) break the shell, uncurl and walk away along the edge of the glass dish. The egg was broken off irregularly, about one-quarter of the shell coming away in two large pieces. The egg measured 7 by 8 mm. and five minutes after hatching the lizard was 38 mm. in total length, the head being 8 mm. When slowly approached the lizard watched intently, its eyes moving independently, but the little creature remained motionless, except for a to and fro motion of the tail tip. This never ceased. When I moved, it scurried off with short, quick darts, the last remains of the yolk sac falling away, while a small bit of shell stuck to its throat for some time. When running, the tail was lifted in a long high curve.

The color was dull bluish-gray, faintly marked with small grayish-white spots on the head, and a series of ten larger separated spots extended in pairs down the back, joining on the rump and becoming bands on the tail. All these spots were preceded by dark areas. The most conspicuous marking, as in the adult, was the transverse prehumeral whitish lines, enclosing a large black spot. Beneath, the color in general was uniform bluish-gray, with the sides of the head, chin and throat marbled with shades of gray. The labials were very conspicuous, black with small, light-colored centers. The pupil was round, the iris with a bright, narrow outer ring of gold, the rest of the iris finely mottled with dull golden brown.

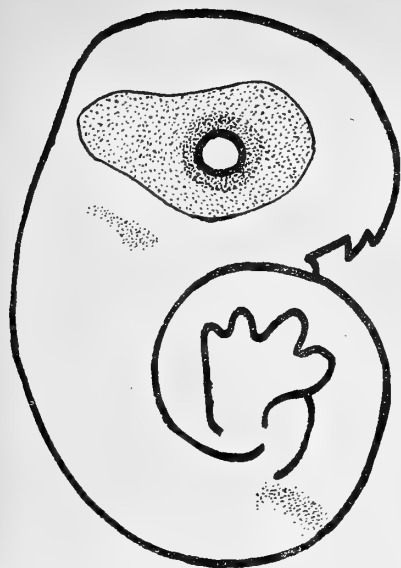
The new-hatched lizard seemed to get grayer and this was seen to be due to the loosening of the epidermis. Within half an hour after emerging from the egg, the skin began to peel off, beginning at the digits and working up the limbs and toward the tail, revealing beneath, intensely contrasting shades of gray and white. Within the first hour the entire skin had been pulled off and swallowed, finishing with a long shred from the tail. Whenever a bit of skin or dirt got on the eyeball, the tongue was run out sideways and quickly passed over the whole eye, thus taking the place of the eyelids.

On July 18, 1920, five eggs were uncovered in three lots in the decayed stem of a spiny palm. (Pl. II, Fig. 4). The shells were hard, smooth and dull white. Weights averaged .15 of a gram, sizes 7 by 7.5 mm. In the case of the two pairs, each egg was separated from its fellow by about a week's development. In the two older ones which were about one-third developed, the embryo, except its head, was completely embedded in the thin yolk. The opaque blue-black eyes were of enormous size, (Text-fig. 4), pear-shaped, half as large as the entire head, which in turn was equal to or larger than all the rest of the embryo. The tail was rolled tightly, the four feet with their short, blunt digits all pressed close together.<sup>2</sup>

On April 29, 1922, an egg was washed out of a hole among roots in the river bank up-river from the laboratory. The embryo was within five days of hatching. This egg was unusually small for this species, 6.7 by 7 mm. The color pattern of the embryo was like the newly-hatched specimen (Cat. No. 229) with the shoulder spot even more emphasized, and in addition a pair of post-sacral, black-and-white ocelli. (Text-fig. 5).

On July 23, 1922, four eggs of this species

<sup>2</sup>This specimen shows, in addition to the large eye, two irregularly linear groups of dark chromatophores, one at the anterior part of the body, behind the eye, and the other at the beginning of the tail. These may very possibly be the first hint of the two pigmental concentrations so distinct in the late embryo.

TEXT-FIG. 4. *Gonatodes annularis*. Early embryo.TEXT-FIG. 5. *Gonatodes annularis*. Late embryo.

were found close together in the débris at the bottom of a decayed bamboo stub close to the laboratory at Kartabo. The shell of these eggs is thicker and tougher than that of a hummingbird. The average size was 6.5 by 7.4 mm. and the weights .25 of a gram.

The first egg hatched August 17, and when 24 hours old the lizard itself weighed .25 of a gram. It had not fed, except on its own skin, and the increase in weight must have been from the absorption of water. A second egg, opened on the same date, was one-third developed. The third egg, also opened on the same date, was four-fifths developed. In this embryo the shoulder ocellus was clearly marked.

The fourth egg hatched on September 13, at least 52 days after the egg was laid. Unlike the newly hatched gecko of August 23, 1919, the skin of this one did not loosen until six hours after emergence, and the method of sloughing was quite different. The epidermis of the entire head, body, limbs and tail became detached, the general color changing quickly to a pale smoky gray. When first observed the loose epidermis was

pushed back from the head, standing out in a ruff close behind the jaws. The gecko crawled about his cage, creeping under the lumps of sawdust and bits of bark in which the eggs had been found, pushing and working till the skin hung in tatters from his body. By turning his head far around, he at last got a piece of this in his mouth and tore off as much as would come and munched it down. He thus gradually freed his body and disposed of the débris, then pushed and rubbed again till the skin at the base of the tail was frayed. He made a tremendous effort, coiling around even beyond a complete circle in order to get a firm grip on the tail covering at its free edge; then he slowly straightened out and the skin peeled cleanly off in one piece, which made his next course. His legs were still completely encased, but he stripped them free very quickly and neatly as gloves are pulled off backward, each little toe covering being perfect as the owner gulped it down. The entire process occupied a quarter of an hour.

I kept the gecko alive for two weeks in a vivarium, during which time I fed it on eight termites. It grew very little. The com-

parative measurements are as follows, the first taken when twenty-four hours old, the second when two weeks of age: Total length 38 and 43 mm., head 6 and 7 mm., tail 20.3 and 22 mm., weight .25 of a gram and 3 grams.

***Gonatodes beebei* Noble, 1923.**

*Name:* Blue-eyed Chestnut Gecko.

*Range:* British Guiana.

*General Account:* This field name, which we used before identification, gives an excellent general idea of the appearance of this lizard. It is known from two specimens and two color plates. The lizards are in the collection of the American Museum of Natural History.

*Type:* N.Y.Z.S. No. 311, American Museum No. 21251, adult male, total length 94 mm., August 26, 1920. Color Plate 215, dorsal view, nat. size, head and neck enlarged; Color Plate 1175, iris. Topotype: No. 38972. (Pl. III, Fig. 5).

Noble's account of the coloring of the type after three years in preservative is as follows: "Uniform reddish brown above, whitish immaculate below, except for a slight suffusion of brown on the abdomen and appendages, this suffusion tending to form dark edges to the scales of the ventral surface of the thigh." His measurements of the type are as follows: "Tip of snout to vent 47 mm., tip of snout to ear 11.5, tip of snout to orbit 5.5, greatest width of head 7, vent to tip of tail 47 mm."

*Color in Life of Type:* Above chestnut shading through orange rufous on the sides to cadmium yellow on the chin and throat, and vinaceous russet on the ventral surface. A scattering of small black dots on back, tail and upper limbs. Iris light cerulean blue, and except for an inner pupil ring stippled everywhere with dark gray. Pupil round.

Caught on a fallen tree trunk in high jungle, five hundred yards from Kartabo laboratory. Kept alive for four days. Quiet, feeding well and amenable to handling. It frequently cleaned its eyes by running its tongue out and over them.

***Gonatodes booni* Van Lidth de Jeude, 1904.**

*Name:* Yellow-spotted Gecko.

*Range:* Known only from Surinam and British Guiana.

*General Account:* On April 15, 1924, I saw a species of gecko new to us, appearing brown and covered with small yellow spots. It escaped all our efforts at capture, running beneath an overhanging bank of earth in the jungle about three hundred yards from the laboratory at Kartabo. A month later, on May 16, I caught the same or another yellow-spotted gecko in the same bank, dig-

ging it out of a twelve-inch hole into which it had rushed. A week later, on May 24, I saw another individual of the same species only ten feet away from where we had taken our specimen. It eluded us. (Pl. III, Fig. 6).

Male breeding (No. 2833, Kartabo, May 16, 1924, Color Plates 740 and 741):

*Measurements:* Length 88 mm., head 12, body 31.5, tail 44.5, head width 8.5, body width 9, eye 2.5, fore leg 17.5, hind leg 28.5, testes 4.5 mm., weight 2.5 grams.

*Color in Life:* Background of upper parts of head and body blackish-brown, covered on head, face, throat, back and upper surfaces of fore limbs with rather closely spaced, irregular spots of empire yellow. These become duller and somewhat smudged on snout and anterior chin. Tail, hind legs and all four feet light russet-vinaceous, mottled with darker. The tail coloration extends up the mid-back in a wide, fairly definite line. Ventral surface primuline yellow under shoulders, shading backward to uniform tawny on under body and limbs, and russet vinaceous under tail. Inner rim of iris cerulean blue, remainder black flecked with light blue. (Pl. III, Fig. 7).

A changing phase of color shows all the spots much more brilliant and intensely orange, and the russet areas become decidedly orange in tone.

The only other specimen known is the type, collected in Surinam and now somewhere in Holland. Its color after preservation is described as "Upper parts dark green, covered all over with larger or smaller lighter spots composed by one, two or more granules of a light green color. Belly lighter without spots; gular region with large greenish spots. Tail without spots, below lighter than above."

***Gonatodes caudiscutatus* (Günther, 1859).**

*Name:* Ladder-back Gecko.

*Range.* Colombia, Ecuador and British Guiana.

*General Account:* No males were seen or secured and only three females. One of these was about to lay an egg on August 25, 1920. The dorsal markings were sufficiently distinct from those of related species to warrant our tentative field name of Ladder-backed, given long before I knew the actual taxonomic species. The vertical white shoulder stripe seems to be placed more posteriorly than in other species. One specimen possessed a very marked ability to change the shade of pattern, the black dorsal markings at night becoming almost invisible. On being annoyed the pattern returned in full strength.

Female adult (No. 598, Kartabo, May 21, 1922, Color Plate 366):

**Color in Life:** General color above grayish-olive, with irregularly longitudinal streakings of dark brown on head. (Pl. IV, Fig. 8). A broad vertebral stripe beginning at base of neck vinaceous buff, extending to insertion of tail. Two small, square patches of black almost meet over the shoulders across the dorsal stripe. The stripe is cut into along each side by nine symmetrical pairs of black points. Shoulder ocellus a large roundish spot of black, surrounded by a band of the general olive background, and this in turn by a still wider black frame, broken only on the posterior rim. Here a crescent-shaped narrow white line extends from the insertion of the fore arm to the mid-back. Side of head olive with fine darker markings and a lateral black line from lores through eye and on backward in a curve above tympanum to shoulder spot. Another black line from upper posterior eye backward and upward to top of head. Lips light olive with a line of black mottling along the lower labials. Limbs strongly mottled with dark brown. Tail with fine, irregular longitudinal markings of dark brown becoming black at tip. Sides of body finely mottled with olive, with two longitudinal lines of dark brown grouped in lengthwise dark spots. Ventral surface dirty white on chin, cream color on under body, mottled with gray under limbs and between fore arms. Under tail salmon buff.

Eyeball ochraceous buff, pupil round, iris dark mottled walnut brown with orange tawny border.

***Gonatodes humeralis* (Guichenot, 1855).**

**Name:** Black Wood Slave.

**Range:** Peru, Brazil and British Guiana.

**General Account:** Only five specimens were found at Kartabo and in the field they were confused with other species of the genus. No unusual habits were recorded, but the dark color was observed as setting them apart. In spite of considerable handling, the tails of this species seemed less deciduous than those of their fellow species.

**Color in Life:** Two types of patterning were observed, apparently distinguishing the sexes. An adult male, length 80 mm. (No. 3084, Kartabo, September 7, 1919) was very dark brown above, slightly paler on chin and throat, becoming still lighter under body and tail. The humeral spot was very faint in life and quite lacking in the preserved specimen. A female, 60 mm. long (268, No. 3117, Kartabo, August 3, 1922) was light brown with a pronounced humeral ocellus, a round, central black spot, surrounded by a ring of pale brown ground color and an outer frame of grayish-white. The back was plain but with a pair of light brown sacral spots, and six wide, pale caudal

bands. Below grayish-white with faint, converging bands on throat.

***Gonatodes ocellatus* (Gray, 1831).**

**Name:** Ocellated Gecko.

**Range:** Northeastern South America, Tobago and Trinidad.

**General Account:** No. 519, and a second in the American Museum of Natural History, No. 38784, appear to be the first recorded from British Guiana. I have no definite notes in regard to habits.

Male, body length 50 mm., tail gone (No. 519, Kartabo, March 21, 1922):

**Color in Life:** General color of head above and on sides and neck Brazil red. Chin and throat brilliant orange. Top and sides of head covered with elongated patches (two running up and back from eye) and markings of capucine yellow edged with black, while on the ventral surface chin, throat and neck these markings are rounded spots. A line of the same yellow extends across the back from shoulder to shoulder, touched with black and slightly broken in the mid-back. General color of sides oil yellow, finely mottled with Brazil red and black. One large and one small ocellus on each side of the body. Broad band down the middle of back and the limbs seal brown. At night the back and limbs change to a frosty gray. Ventral surface dusky slate violet, except for a small patch of terra cotta at base of neck and a median line under the tail of pompeian red. Pupil round, iris rim apricot buff, remainder hazel with dark stippling.

***Gonatodes vittatus* (Lichtenstein, 1856).**

**Name:** Gray-striped Gecko.

**Range:** Colombia to British Guiana, Trinidad and the Dutch Leeward Islands.

**General Account:** These geckos were of so indefinite a pattern and coloration that in the field they were not given a name or set apart from the females of *annularis*. At least five individuals were recorded, taken March 28, 1919 (2 specimens), July 4, 1920, July 16, 1920 (2 specimens), and June 4, 1922.

***Sphaerodactylus molei* Boettger, 1894.**

**Names:** Black-and-white-headed Gecko (male), Orange-tailed Gecko, Gray-headed Gecko (female); Striped Wood Slave (Guiana Creole name); Shallee-shallee (Akawai Indian).

**Range:** Northeastern South America and Trinidad.

**General Account:** This gecko shares with the larger *Thecadactylus* whatever advantages are yielded by life in human buildings. It was often found in both our Kartabo and Caripito laboratories, running at night over the walls and up the legs of our tables. It

creeps very slowly when stalking prey and at other times runs with short, quick darts. When frightened its short legs become inadequate, and progression is by a frantic sinuous wriggling, almost *Leposoma*-like. The tail breaks off very easily and the break is clean with almost no muscle ends showing, and on the body end there is usually sufficient overlapping skin to fold in and almost hide the fracture. The tail end, reasonably enough, is less protected by excess skin.

I made no detailed observations on the shape of the pupil in this species, taking for granted that it is always round, but in several photographs taken immediately after death one or both pupils appear as slightly vertical.

Male breeding, body 25 mm., tail 29 (No. 209, Kartabo, April 5, 1919, Color Plate 163).

*Color in Life:* Top and sides of head and neck jet black variegated with creamy white, chiefly in the form of two broken lines from the nostrils back over the eyes, forming an indefinite "Y" on the neck. (Pl. IV, Figs. 9, 10 and 11). Also a solid broad white line from the eye back to the abrupt ending of the black nuchal area in front of the fore limb. Body buffy green. Limbs very light, dotted thickly and irregularly everywhere with dark brown. Tail abruptly ochraceous-orange, the color resulting from many large spots set close together both above and below. Rostral, all labials, lower side of head and neck, the chin and throat yellow-green, remainder of ventral surface of body creamy-white. Pupil round, iris ivory white, finely dotted with large, dark brown crescentic marks, especially dense in front of and behind the pupil.

A 49 mm. male taken April 11, 1919, wholly lacks the central dorsal cephalic white spots, and the body freckling is confined to the sides and pelvic region.

Male, not breeding, body 25.5 mm., tail 27.5 mm., (No. 538, Kartabo, April 13, 1922, Color Plate 358):

*Color in Life:* General color above deep olive buff tinged with apricot orange on head and merging on the tail into capucine yellow. Groups of tiny picric yellow dots on orbits and before and behind orbits in vague lateral lines. All upper surfaces covered with scattered small spots of pecan brown, very faint on neck and fore limbs. These spots become heavier and darker brown on posterior body, and still heavier and more irregularly spaced and elongated on anterior tail. Beyond mid-tail they die out, the remainder being faintly mottled with gray. The dorsal spots arrange themselves either side of a plain narrow vertebral line, giving the effect of a dorsal body stripe. Side of

head primuline yellow. Broad lateral stripe of picric yellow from eye diagonally upward to sides of neck. This marking is strongly edged with black along each side, which color in turn shades into orange outer bands. The lower band extends forward through the eye, becoming fainter on the snout. Chin lemon chrome; ventral surfaces maize yellow. Under tail zinc orange. Toes grayish.

Pupil round. Inner iris rim ivory white. Rest of iris white with grayish stippling on outer edges. Fore and aft a wide band of walnut brown continues through the iris the loral-postorbital band.

Female, not breeding, length 46 mm. (No. 209a, Kartabo, April 11, 1919):

*Color in Life:* In general buff with the head and neck rather indefinite gray. Apparently unmarked except for two light flank lines, down each side of the dorsal pelvic region. In the right light, however, all the broad cephalic lines of the male are visible as lighter brown—i. e., the two lateral lines and the central "Y". The lateral lines extend very faintly down the body and, becoming strong at the pelvic zone, die abruptly at the caudal change to coarser imbricated scalation, which marks the area of regeneration.

*Color in Life of Young:* Young geckos show a uniform pattern. Many, such as one 30 mm. in length, taken May 4, 1922, are light buffy brown, with no trace of the dark cephalic bands of the adult. Two wide, pale brown bands start from the eye and extend back just above the limbs to the tip of the tail. These are faintly bounded with black. Here and there down these lines and also down the center of the back, are very small, brilliant, isolated yellowish-white scales. On the posterior half of the tail these increase in number, gather some black scales about them and form four light bands, the tip of the tail being almost white with a black sub-terminal band.

A very young gecko, 23 mm. total length, May 16, 1919, has the head dark grayish, body and tail olive. The eye to tail tip bands are very pronounced. There is a row of small, pale vertebral dots. Near the base of the tail are two pale lateral spots; beyond these a second pair almost join, and still farther are three pale creamy white bands, the most conspicuous markings on the young lizard. At night all markings except these caudal bands disappear.

*Food:* Small, winged wood roaches, red mites, ants and termites.

*Enemies:* On the night of July 3, 1920, by flash-light I surprised a ghostly white *Thecadactylus* on a jungle tree trunk with a small gecko in its mouth. My quick grab secured only the victim and the wriggling tail of the larger lizard. The unfortunate



gecko proved to be a 28 mm. *Sphaerodactylus molei*.

**Breeding:** No. 1934 was an oval egg, 5 by 7 mm., collected July 30, 1919, in a rotten stump, together with the female lizard which was about to deposit a second fully-formed egg. The egg in the sawdust was very stained and slightly dented, so I thought it was bad, but the embryo proved to be in perfect health and would have hatched in three or four days. It was packed tightly in the shell, and measured 33 mm. in length over all. The color was a dull mottling of several shades of brown with the two lateral body lines and caudal black and white bands well marked. Four separate times I placed it in absolute darkness in the photographic room, examined it after returning it to the light, and then re-examined it after exposure to strong daylight. In each case the gray mottling and to a less extent the lateral body lines became so faint that they were barely discernible. There was no change in the caudal bands. The embryo lived for five hours, and the color change tests were carried on in the first half hour, before I removed the lizard and measured it. In the case of this female there was a single large egg in the oviduct, and no trace of a less developed second. This was the case in three other instances, but not with gecko No. 2652, adult female, body length 28 mm., taken March 16, 1924, which was about to shed its skin. When I dissected this specimen I found two fully formed eggs about to be laid, 5.5 by 7 mm. The lizard was of typical color, buffy brown with gray head, and faint head lines.

***Hemidactylus mabouia*** (Moreau de Jonnes, 1818).

**Name:** White Gongasacka.

**Range:** Northeastern South America including Brazil, and the Antilles.

**General Account:** No notes were made of this species except that at least two specimens were taken, one of them in July, 1920, in the laboratory at night, appearing dead white unmarked even by black tail bands. No. 195 was found on a tree trunk September 25, 1917. In general large size and in the peculiar character of the vertical pupil this gecko recalls *Thecadactylus* rather than any of the genera of small lizards.

***Thecadactylus rapicaudus*** (Houttuyn, 1782).

**Names:** Large House Gecko, Cat-eyed Gecko; Gongasacka (Guiana Creole Name); Cang-gah-sah or Kingasah, "One-who-calls-in-the-house" (Akawai Indian).

**Range:** South America except southern part; Central America and the West Indies.

**General Account:** Almost anywhere in the warmer parts of the neotropical region,

when human beings first occupy a house they will find that two small native creatures have preceded them. One is the little tree frog, *Hyla rubra*, who considers the kitchen sink or a bath tub or rain barrel the equal of any jungle home. The other is the gray house gecko, *Thecadactylus rapicaudus*. Both are perfectly harmless, they are nocturnal, they can cope with smooth perpendicular surfaces by means of vacuum soles to their feet, and both have pleasant voices which are heard, now and then, throughout the night.

The cat-eyed gecko is common both at Kartabo and Caripito. Its normal haunts are decayed logs and hollow trees, and it also approves of the cavities behind the leaf stalks of palms. Half a dozen were always to be found in the laboratory at Kartabo, hidden away in solitary obscurity during the day, but creeping forth when our insect-attracting lamps were lit.

Out of dozens of these geckos collected, the following measurements of a male with a perfect tail are average. They are percentages of total length. No. 201, Kartabo, adult male, Dec. 23, 1920: Total length 144 mm., body 53 per cent., head 18, head width 10, snout to eye 7, eye diameter 3, fore leg 16, hind leg 21 per cent., weight 9.3 grams.

**Color in Life:** Adult. The thirteen words with which Boulenger (*Catalogue of the Lizards in the British Museum*, I, p. 112) characterized this gecko can hardly be improved upon. "Brown or greyish-brown above, variegated with darker and lighter; lower surfaces whitish, immaculate."

The variety of mottling and spotting in adult geckos is infinite. The most consistent marking is the olive buff of the labials, and a broad, irregular, pale olive-brown stripe from the eye to the shoulder, bounded above and below by equally wide bands of dark brown. The complexity of the pigmental characters in general is increased by the occasional temporary appearance of fairly regular bars and spots down the back, at times when the creature is excited or alarmed, with a subsequent return to the heterogeneous pattern of calmer emotions. The tail is the most variable part, if such a superlative is possible, and no two are alike. Some are lined with a multitude of thin, hairlike, dark streaks, or waved indefinitely with several shades of gray or brown, or a dark background will have broken bands of lighter. Regenerated tails are usually without definitely contrasting markings. Immature geckos often show very regular markings, such as No. 30,009, under the next heading.

**Change of Color:** Temperamental change of color is sometimes very marked, but is never so radical as that from diurnal to

nocturnal color and pattern. This is especially pronounced in young and half-grown individuals. Typical was the change in No. 30,009 (Caripito, March 15, 1942, Color Plate 1508.) This immature specimen, which measured 125 mm. over all, was captured in the jungle under bark. In general it may be called vinaceous, with the top of the head, limbs and dorsal markings of body and tail light wine-colored, elsewhere darker. The two most brilliant areas are the golden eyes, and a narrow, single-barbed dead white line from the eye back along the side of the head. The head is coarsely dotted, the limbs blotched with dark vinaceous. Down the back are very conspicuous markings, light violet, divided narrowly into three, each of which may be described as a broad arrow head, directed posteriorly, with two extra pairs of barbs down its shaft, all surrounded and emphasized by a frame of black. The basal half of the tail has three wide bands of light violet, then an exceedingly wide band of black and a pale tip. (Pl. V, Figs. 12 and 13).

The lizard escaped in the laboratory and when caught late in the evening bore no pigmental resemblance to its diurnal phase. The whole animal had become pale pinkish-white, except for the dorsal markings which had paled to ivory white. The two conspicuous exceptions to this fading were the eyes and the broad black tail band which remained a broad black tail band.

Color change in another individual was less marked. A female, 112 mm. in total length, every night at 8 o'clock turned a brownish-white, with several small, irregular dark marks down the tail, marks which were quite absent in the diurnal patterning. After having been covered all night, at 6 in the morning the color was unchanged except for a decided tinge of olive green. After ten minutes' exposure to daylight the green increased in intensity, and a dark ground color began to appear, a deep olive brown, lighter colors being confined to irregular streaks on the head and a series of haphazard spots down the back. This sequence of color change was always the same whether the lizard was uncovered at 8 A.M., noon or 3 P.M. The change was unaffected by the regular rhythmic change of the twenty-four hourly shift from light to darkness, but influenced only by direct illumination on the gecko.

*Tail:* This organ is strongly prehensile, and when the lizard is clinging motionless to glass, the belly and tail are pressed so closely against the surface that it seems as if they must give material aid to the vacuum feet. Yet this gecko can walk on a dry, vertical glass surface with the body and tail raised clear. At moments of excitement the

tail is curved high in the air and waved slowly to and fro, doubtless as lure or bait to any enemy; an easily dislocated "pound of flesh" offered in exchange for the chance of escape. When the tail is detached there ensues a frantic twisting and wriggling, so violent that the entire tail flicks into the air again and again, before it slowly dies its isolated death.

The base of the tail is swollen and the ultimate zone of possible fracture begins at the posterior end of this swollen area, about 10 mm. behind the anus. On each side of the vent is a double tooth or spine-like scale. The regenerated tails lack much of the prehensile and coiling ability of the original and can never lie as flatly and as closely applied to any surface.

*Eye:* The eye of this gecko is magnificent. (Pl. V, Fig. 15). It is very large, adapted for nocturnal sight, perfectly round and with the lids reduced to tiny folds. The nictitating membrane, which is crumpled into a useless fold in our own eye, is here a convex "watch crystal" of hard, transparent tissue within which we can see the eye ball rotate freely. But though lids are absent, yet the eye is protected from excessive light by the great mobility of the pupil. In daylight there is visible only a narrow, vertical slit with opposing nicks which when pressed together leave four very small diamond-shaped openings, admitting sufficient light for the detection of danger and the performance of all necessary activities. The rest of the eye, the iris, in breeding males, is a splendid ball of glowing coppery gold, shot and zigzagged with veins of rich warm brown. In most females and less developed males, the iris is bright silver.

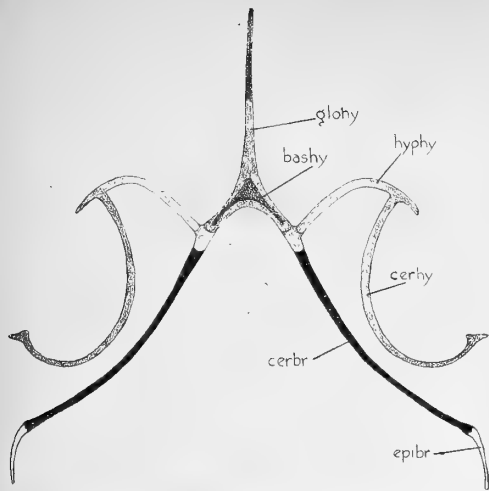
*Tongue:* The tongue is moderately protrusible and mobile. When some sudden alarm has passed the gecko will often "lick its chops" six or eight times, the tongue curling up and over the lips. In males in full breeding condition (No. 2923, Kartabo, Plate 759) the rounded tip of the tongue is a conspicuous bluish-violet. Vague hints of an elaborate courtship which have come to notice make it possible that these lingual colors may play a part. As in other geckos, the tongue functions as eye-lids and from time to time is passed over the eyes, cleaning them of any dust or other detritus.

Male, length 135 mm. (Kartabo, KOH No. 2034, July 5, 1920):

*Hyoid:* Characterized by the pronounced curve of the ceratohyal and the absence of any hint of a second branchial arch.

The basihyals send forward a long, slender lingual process, the glossohyal. The posterior bifurcations of the basihyals are wide spread, but short and not very thick. A tripointed core of dense cartilage marks





TEXT-FIG. 6. *Thecadactylus rapicaudus*. Hyoid.  
x5.

the juncture. The hyoid and first branchial arches arise from the tips of the basihyals, the former at right angles, and the latter continuing the arms of the basihyal forks. The hypohyals are wholly cartilaginous and bend sharply out and backward, ending in a hyaline tip. At right angles posteriorly to this transparent tip, arise the ceratohyals, long, slender and cartilaginous, and bent outward and upward into the form of an inverted half heart. The distal extremity is widened and flattened into a shoe of considerable size. The first branchial arch continues the line of direction (obliquely backward) of the basihyal bifurcations. This arch consists of the ceratobranchial, a very long, slender, outcurving rod with a strong core of bone. At the proximal point of juncture there is a tiny nodule of bone, representing the hemispherical cap of *Sphaerodactylus* and *Neusticurus*; probably the remains of a hypobranchial. The ceratobranchial terminates in a separate, slender, pointed segment of hyaline cartilage representing the remains of the first epibranchial. *Measurements*: Basihyal length 1.7 mm., width of forks 2.2, hypohyal 2.5, ceratohyal length (measured straight between tips) 4.5, ceratobranchial length 8 mm.

Checked with a second specimen, No. 3081 from Caripito, no difference is seen except that the ceratohyals are considerably less curved, more nearly parallel with the ceratobranchials. In this specimen, too, the end of the epihyal makes a narrow loop and connects directly with the area near the auditory apparatus. The more curved character of the ceratohyals in the Kartabo lizard may well be a mechanical contraction owing to loss of otic connection

and a subsequent lessening of longitudinal strain.

*Feet and Progression*: (Pl. VI, Figs. 16 and 17). The movements when these geckos are undisturbed are very slow and deliberate, recalling the ponderous progress of an elephant, the very antithesis of the nervous, waving, shaking little hands of a *Cnemidophorus* lizard. The raising and lowering of the feet is an interesting proceeding. At each step the whole foot is pressed down firmly, but without any sudden or abrupt movement, and there is nothing to indicate that the sub-plantar, vertical plates are developing most efficient vacuums. The loosening of this grip is amazing and unexpected, one which gives the same shock as the abnormal, boneless-appearing feats of an accomplished acrobatic contortionist. Starting with the very tips, all five toes slowly curl and roll up and back, until they are curved flat against the wrist or ankle, transforming the pentadactyl foot into a small, compact round ball whose surface is composed of backward-curved lamellae. The limb advances, is pressed down again and all five toes uncurl and are placed firmly on bark, wood or glass, as the case may be. This performance is completely lost to the eye when the gecko moves rapidly. We can illustrate what takes place by assuming that the back of our hands are the palms, and then walking them along a table top, with fingers extended and curled tightly in turn. Before I ever saw this in life I wondered why these lizards so often died with their digits curled far backward. Judging by the similarly flexed toes of preserved *Hemidactylus mabouia*, I should expect to find the same method of devacuation.

*Voice*: Now and then in the night we hear the call of this gecko in the laboratory at Kartabo, a high, rapidly reiterated *chick-chick-chick* or *chack-chack-chack*, fifteen or twenty times repeated, much like the note of some insect. It seems possible but not probable that besides being a sexual call this may be mimetic, alluring insects which may have somewhat similar notes. I should guess that the sound is mechanical, produced by some action of tongue and palate.

*Food*: These geckos will eat almost any insect they can catch. Several individuals learned to come every evening to our laboratory tables at Kalacoon and take small moths from the tip of our forceps. I once fed two of them some immature vile-smelling hemiptera and while the insects were swallowed, it was with reluctance and with subsequent licking of lips and rubbing of the sides of the mouth. The insects were very decidedly distasteful.

At Kartabo I once heard the clatter of an empty cigarette tin and the racket keeping up I went to investigate. The tin appeared to be jiggling about under its own steam. Beneath, I found a large gecko and a winged roach of largest size in a rough-and-tumble fight, which kept up after I had exposed them. The lizard had the insect by the head, but the great flapping wings prevented further ingestion for some time. The tin had been disturbed and fallen over the combatants but had not interfered with the row.

The stomach contents of four Kartabo geckos were as follows: (1), termite worker, beetle, red mite and moth fly; (2), many small insects and several spiders; (3), mollusk shell, small beetle, 3 moths, 2 flies, 2 flying ants; (4), 3 small wood roaches and 4 moths.

*Fighting and Courtship:* Whenever a full-grown gecko meets a small one of his own species, the latter shows his nervousness by a tremulous waving of the tail and any continued threat of approach results in headlong flight. Three separate times I saw adult geckos meet each other by accident in the laboratory, when there ensued much vigorous tail waving and licking of lips on the part of one, while in the other these actions were absent or were kept in low gear. On one occasion, one of the two *chack-chacked* three times in quick succession. Either because of my presence or the illumination from my lamp or flash, nothing further resulted.

*Enemies:* I can tell of only one enemy, and that of my own contriving. On April 6, 1919, I placed a *Thecadactylus* within reach of a pet cebus monkey. It was seized and when the tail fell off, the lizard was dropped and the monkey concentrated on the wriggling, dancing tail, which he grasped and ate. Ultimately he also caught and devoured the more quiescent owner, which had failed to make the most of his opportunity and get beyond the radius of the tethering chain.

*Breeding:* Female No. 3282, Kartabo, August 25, 1922, laid an egg in her vivarium. It was a very broad oval, 13.4 by 11.4 mm. and weighed 1 gram. The shell was hard and white originally, but when found it was completely covered with a fine mosaic of debris, bits of quartz, cast gecko skin and insect remains, giving it the appearance of a finely mottled, gray-brown egg. The debris was sunk deep into the shell structure and firmly fixed, as if the surface had been soft when the egg was laid, perhaps also mucilaginous, and the egg had been rolled about until thoroughly encrusted.

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## EXPLANATION OF THE PLATES

## PLATE I.

- Fig. 1. *Gonatodes albogularis*. Head and shoulder.  $\times 3.5$ .  
 Fig. 2. *Gonatodes albogularis*. Natural size.  
 Fig. 3. *Gonatodes annularis*. Head and fore body.  $\times 5$ .

## PLATE II.

- Fig. 4. *Gonatodes annularis*. Four eggs in a bamboo stub.

## PLATE III.

- FIG. 5. *Gonatodes beebei*. Head.  $\times 2.7$ .  
 Fig. 6. *Gonatodes booni*. Natural size.  
 Fig. 7. *Gonatodes booni*. Head and fore body.  $\times 5.6$ .

## PLATE IV.

- Fig. 8. *Gonatodes caudiscutatus*. Head and fore body.  $\times 8.3$ .

- Fig. 9. *Sphaerodactylus molei*. Natural size.

- Fig. 10. *Sphaerodactylus molei*. Head enlarged, dorsal view.  $\times 2.5$ .

- Fig. 11. *Sphaerodactylus molei*. Head enlarged, lateral view.  $\times 6$ .

## PLATE V.

- Fig. 12. *Thecadactylus rapicaudus*. Day coloration.

- Fig. 13. *Thecadactylus rapicaudus*. Night coloration.

- Fig. 14. *Thecadactylus rapicaudus*. Natural size; renewed tail.

- Fig. 15. *Thecadactylus rapicaudus*. Head and fore body.  $\times 2.6$ .

## PLATE VI.

- Fig. 16. *Thecadactylus rapicaudus*. Sole of foot.  $\times 7.6$ .

- Fig. 17. *Thecadactylus rapicaudus*. Toes re-verted.  $\times 2.2$ .



FIG. 1.



FIG. 2.



FIG. 3.

FIELD NOTES ON THE LIZARDS OF KARTABO, BRITISH GUIANA, AND CARIPITO, VENEZUELA.





FIG. 4.

FIELD NOTES ON THE LIZARDS OF KARTABO, BRITISH GUIANA, AND CARIPITO, VENEZUELA.





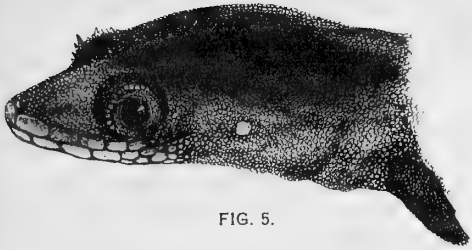


FIG. 5.



FIG. 6.



FIG. 7.





FIG. 8.

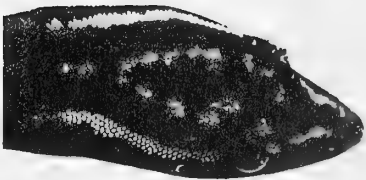


FIG. 10.



FIG. 9.

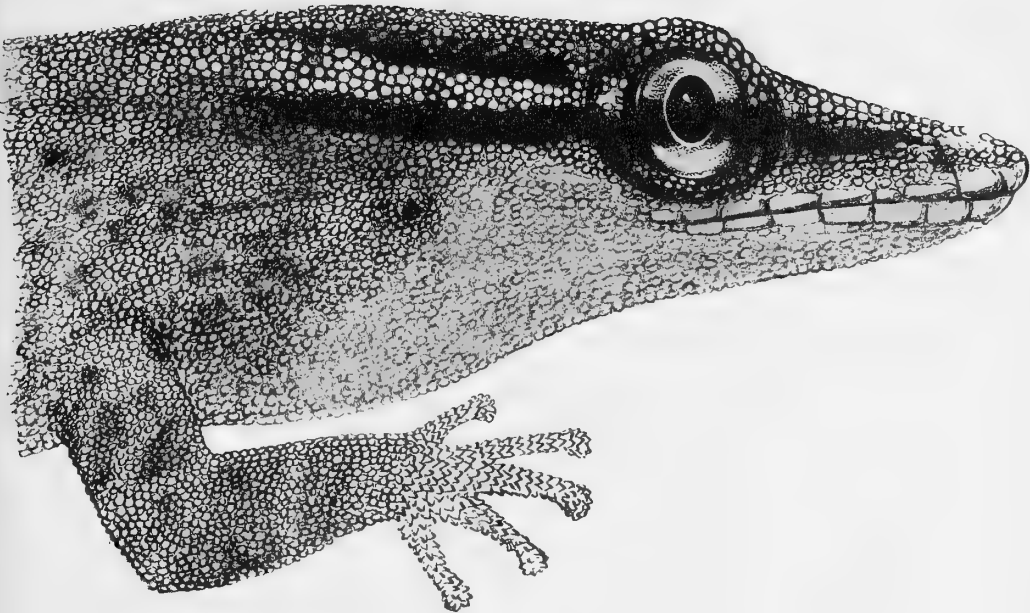


FIG. 11.

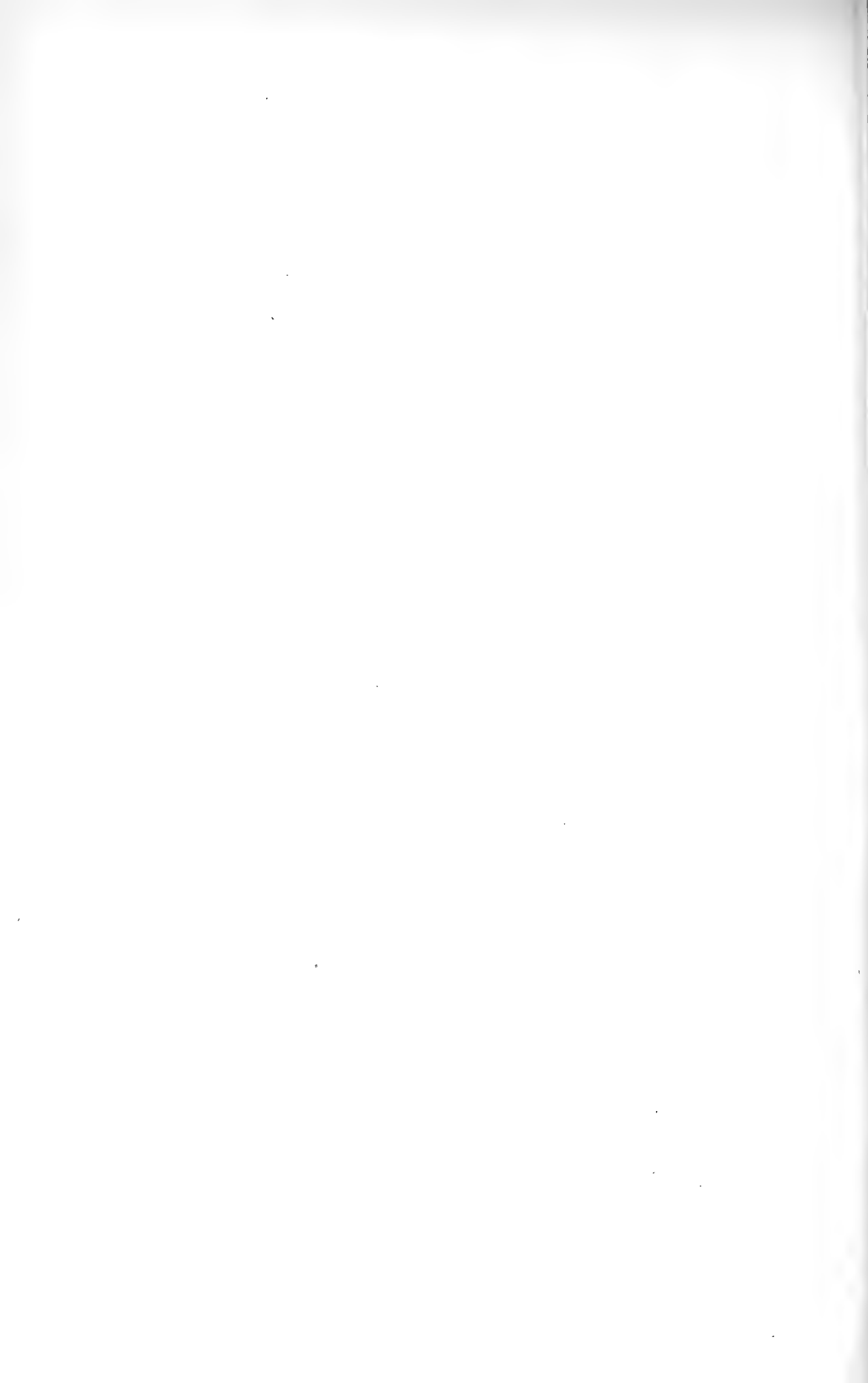




FIG. 12.



FIG. 13.



FIG. 14.

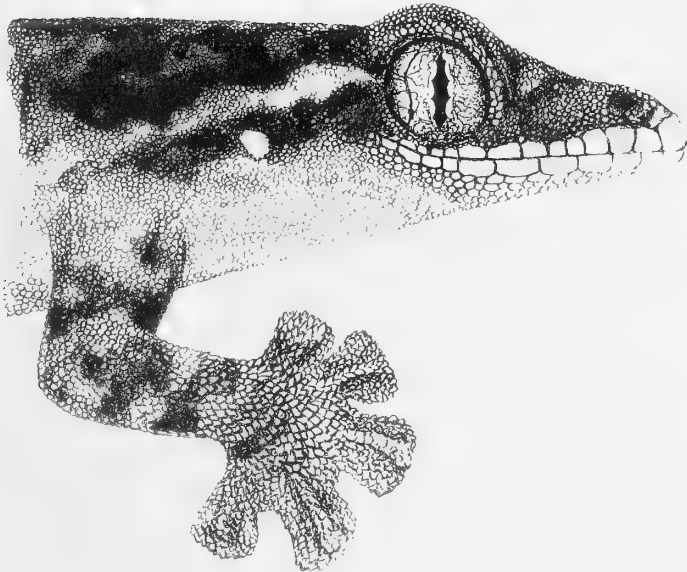


FIG. 15.



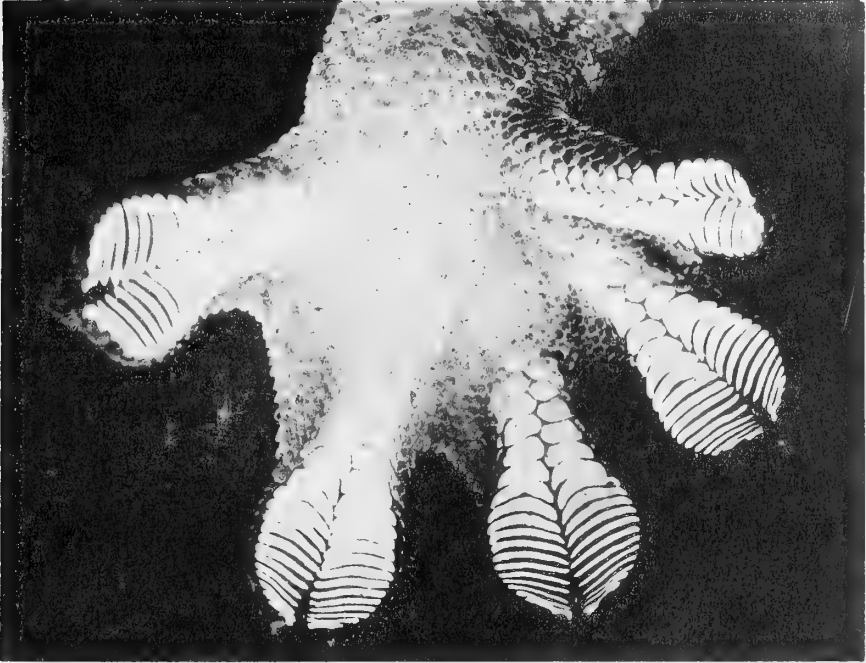


FIG. 16.

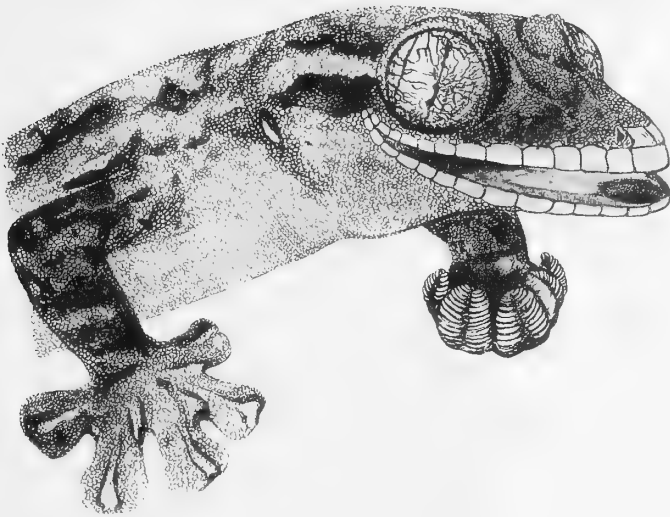


FIG. 17.

FIELD NOTES ON THE LIZARDS OF KARTABO, BRITISH GUIANA, AND CARIPITO, VENEZUELA.





## 15.

On the Color Changes of Fiddler Crabs (Genus *Uca*) in the Field.<sup>1</sup>

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[This is a contribution resulting from a trip made in the spring of 1944 to Venezuela, Colombia and Ecuador, under the auspices of the New York Zoological Society and the Committee for Inter-American Artistic and Intellectual Relations. Invaluable assistance was received from Dr. William Beebe, Director of the Department of Tropical Research, the Creole Petroleum Corporation, Mr. and Mrs. William H. Phelps and Mrs. Sherman P. Haight.]

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## I. INTRODUCTION.

During the past few years a number of investigators have done a great deal of excellent experimental work on the role of secretions from the crustacean eyestalk sinus gland and central nervous organs in chromatophore activation. Fiddler crabs have been frequently employed with great success as the subjects of the experiments. None of this research, however, by its very nature could be done on animals living in natural surroundings, and all was performed on three western Atlantic species, *Uca pugnax*, *U. minax* and *U. pugilator*, none of which shows the high degrees of color development found in some tropical forms during display. Our own previous observations (1941, 1943.1, 1943.2) indicated both the importance of the natural habitat in bringing about the crab's most extreme color changes and the great diversity of color development within the genus. Therefore it seems worthwhile to present certain more recent observations, summarize the

field color studies, and correlate these as much as possible with the results of the laboratory investigators. By this means it is hoped that directions will be suggested for future research, preferably in ideal combinations of experimental endocrinology with observation in the field. My thanks go to Dr. F. A. Brown, Jr., for his helpful comments via personal letter on some of his unpublished observations.

Kleinholz (1942) and Brown (1944) have published the most recent and comprehensive surveys of our present knowledge of crustacean hormones, including the mechanism of chromatophore control. For detailed discussion of the subject and extensive bibliographies, reference should be made to these papers. For the purposes of this discussion, the following brief résumé may be made of the aspects immediately related to the present subject.

A. *Brachyuran Chromatophores*: It is known that in brachyuran crabs most external pigment is located in monochromatic chromatophores which are found chiefly in the epidermis. They have permanent branching processes, so that the pigment may be either concentrated in the chromatophore's center, in which case it is scarcely or not at all perceived in the macroscopic coloration of the crab, or it may be widely dispersed into the processes. Four pigments occur in crab chromatophores, all of which are found in *Uca*: black or brownish-black (probably a melanin; hereafter called simply "black"), red, yellow and white (perhaps guanine). A fifth crustacean pigment, a blue, is the only one found outside of the chromatophores; it has not been investigated in *Uca*, although blue is of frequent occurrence in the genus.

All of the striking specific color differences noted when fiddler crabs are studied in the field may be explained by the assumption that each species contains these five pigments in varying proportions, distribution and states of dispersal. Research, however, has scarcely begun on this question: Carlson (1936, p. 67), working with *pugilator*, found red chromatophores fewest of all

<sup>1</sup> Contribution No. 695, Department of Tropical Research, New York Zoological Society.

kinds, but still numbering half as many as the abundant black; Abramowitz (1937) found, on the other hand, that in *pugnax* red is usually lacking. A connection between localized white chromatophores and breeding condition has been demonstrated in female shrimps (*Leander*) (Knowles & Callen, 1940), and similar seasonal influences will almost certainly be found to apply to some pigments in *Uca*. Doubtless there will prove to be differences of specific rank in amount or potency of hormones affecting the dispersal of pigments, of importance equal to or greater than the actual number of chromatophores or amount of pigment within them. At present, however, nothing whatever is known of these aspects.

*B. Hormonal Activators of Chromatophores in Uca:* Two sources of chromatophoretropic hormones are at present known to exist in fiddler crabs, the sinus gland of the eyestalk and the central nervous organs. The hormonal principles in the sinus gland, numbering at least two, are responsible for the dispersal of the black, red and perhaps the white chromatophoral pigment, and the concentration of the yellow and perhaps the white. One or more principles from the central nervous organs bring about the dispersal of both the black and the white, as in the case of the sinus gland, according to an unpublished paper by Brown & Cunningham (Brown, 1944, p. 131, and personal communication). The known effects in *Uca* may be expressed in Table 1. The influence of hormones on the blue, probably extra-chromatophoric, pigment is omitted because of lack of data.

TABLE I. CHROMATOPHORE CONTROL IN *UCA*.

Origin of Hormone (s)	Effect on Chromatophores			
	Black	Red	Yellow	White
Sinus Gland .....	D	D	C	D and/or C
Central Nervous Organs .....	D	?	?	D
Key: D—Disperses				
C—Concentrates				

The function of these control systems in nature has scarcely begun to be explored. Brown considers it almost certain (1944, p. 131) that the diurnal rhythm of fiddler crabs (see below), which continues to a certain extent regardless of light intensity or loss of eyes, is controlled by secretions from the central nervous organs. No function has yet been assigned, however, to the color changes controlled by sinus gland principles. In the following pages possible connections between endocrine functions and natural color change are suggested, and some aspects of the development of color in the group discussed.

II. COLOR CHANGES OF *UCA* IN THE FIELD.

In Table II is given a list, compiled from field observations on more than 20 species, of the apparent motivation of color changes as they occur in nature. All except those on diurnal rhythm, which have been well established by previous observers, are the result of our own field work carried out chiefly in the American tropics; they apply to a lesser extent, however, to the three northern Atlantic species mentioned above. Here only darkening and lightening are indicated, regardless of the chromatophoric principles involved.

TABLE II. COLOR CHANGE IN *UCA* IN THE FIELD.

Time, Place or Condition	Crab Darkens	Crab Lightens
Day	X	—
Night	—	X
Submergence in burrow	X	—
Capture and holding	X	—
Display	—	X

These color changes will be discussed in order. Since individual *Uca* show little or no adjustment to background color, that adaptation, so characteristic of many crustaceans, is not considered in the present paper.

*A. Diurnal Darkening.* It is well established that normal fiddlers are somewhat darker during the day than at night, and that this rhythm continues to a certain extent regardless of whether the crabs have been blinded, their sinus glands removed or both (see especially Abramowitz & Abramowitz, 1938, and Brown, 1944, p. 131). As

mentioned above, the diurnal rhythm is probably controlled by principles from the central nervous organs, which during the day-time disperse the black pigment. As there is no evidence that the white is dispersed at night, the nocturnal lightening appears to be due to the simple concentration of the black, particularly on the legs and ventral surface. It is much less intense than the dazzling white assumed by some species in display, which often extends over the entire body and, more rarely, the appendages as well. As has long been known, *Uca* is altogether diurnal; at night it never feeds, digs or waves, and rarely even

emerges from its burrow, although it may sit in the mouth during nocturnal low tides. A day-time darkening is of conceivable practical benefit in making the crab inconspicuous in its usually dark muddy-sand or muddy habitat.

**B. Submergence Darkening.** A fiddler crab in light display coloration (see below) is darkened slowly by prolonged submersion in its damp burrow. Hence the principle responsible for this type of darkening—whether originating in the sinus gland, the central nervous organs or elsewhere—obviously inhibits the effect of the display-brightening mechanism. This darkening appears more extensive than could be explained merely by the saturation of the cuticle and its resulting translucence, which would permit body organs to show through. Also, it is quite different from the superficial effect caused by clinging mud or sand. Since the display-brightening mechanism inhibits the diurnal rhythm presumably motivated by the central nervous organs, it is likely that the darkening principle of the sinus gland will be found to be responsible for the dispersal in burrow submersion. Any benefit to the crab is hard to imagine; it seems more likely that this effect will prove to be a psychological by-product connected with some other process—perhaps to activity of the gland in some branch of metabolism concerned with respiration or water-intake. In fact, this darkening is perhaps a slight disadvantage, if, as seems almost certain, display-brightness has recognition, advertising and/or stimulating value; a darkened crab must lose precious low tide display time in regaining brightness. No darkening effect is seen after brief descents, caused by momentary alarms, occasional digging activities, or the need for moistening the gills. It is extremely only after prolonged digging and after submergence during high tide.

**C. Darkening on Capture.** A similar darkening effect is seen when a crab in display coloration is seized and held in the hand, only in this case the darkening is usually much more rapid than when the crab merely descends into its burrow. The time required for the change is highly variable in species and individuals. So far, it has appeared most rapid in *U. latimanus*, one of the species in which display-blanching is most highly developed. The incidental effect of adrenalin on some vertebrate chromatophores during emergency may be kept in mind for possible parallelisms among fiddler crabs, especially in view of the similarity already suspected (Brown, 1944b, p. 133) of crustacean central nervous organ extracts to adrenalin or acetylcholine. If a *Uca* nervous organ principle is responsible, however, for “emerg-

ency” darkening of display coloration, it is probably different from the diurnal-darkening principle, since the latter is inhibited by the display-brightening substance.

It may be remarked here that we have not so far succeeded in inducing either display-coloration or waving in any fiddlers with pronounced display colors (e.g. *U. stenodactyla*, *styliifera*, *saltitanta*, etc.) kept in captivity, although these experiments have not yet been carried out systematically.

**D. Display Brightening.** The lightening, often to dazzling whiteness, of fiddlers in the breeding season and, during that season, of displaying individuals on bright days at low tide, has been repeatedly observed by us in both temperate and tropical species in the western hemisphere. For unknown reasons, the effect appears to reach its highest development in the tropical eastern Pacific. Its general characteristics have been previously discussed (Crane, 1941, pp. 154 ff). In regard to the chromatophoral hormonal aspect, which has yet to be investigated experimentally, the following remarks may be made:

1. One or more principles must be active which inhibit the normal effect of the central nervous organ principle which is apparently responsible for diurnal darkening as well, perhaps, as the dark-dispersing principle of the sinus gland, the function of which is so far unknown.

2. The same or other principles must be responsible for the maximum dispersal of the yellow and white pigments, which are chiefly concerned in the brightening, as well as those bringing about the occasional subsequent concentration of the yellow (see p. 165), and special display coloration such as bright red chelae, purple ambulatories and bright blue eyestalks.

3. Since this maximum brightening occurs in the display season, which is intimately connected with breeding in at least a majority of species, it is likely that sex hormones, produced in the gonads or elsewhere, will be found to be responsible.

4. At least one immediate source may prove to be a dispersing-white principle of the sinus gland. The existence of this principle is recorded by Brown (1944, p. 40) as an unpublished observation, although Abramowitz (1937) has considered it as a concentrating-white agent.

5. Although no sex hormones have yet been proved to exist in Crustacea, the white chromatophores appearing in egg-bearing segments of female *Leander* should be kept in mind in attempting to explain the display colors in *Uca*. Knowles & Callen (1940) found that these chromatophores failed to develop in *Leander* which had been parasitized or X-ray castrated, but think that little

evidence was thus given for the existence of a female sex hormone. Their preferred, alternative conclusion is that these white chromatophores are a by-product of the increased metabolic rate of the breeding season. Some such relatively simple explanation as the latter may prove to be true in *Uca*: The same authors remark on the part known to be played by guanin accumulations in the nuptial coloration of many vertebrates. Another phenomenon, reported by McVay (1942) working with *Cambarus*, may prove to have a bearing on the problem: she reports a seasonal change in the concentration of the white chromatophore-contracting principle from the brain of females, and a striking difference between males and females in the total amount present. It is likely that the seasonal behavior of white pigment in the three crustaceans—shrimp, crayfish and fiddler crab—will prove to be related. Should a basic excretory origin be proven, an adaptive use of the resultant white pigment as a recognition and stimulatory device in *Uca* would not of course be necessarily eliminated.

Some further aspects of display-brightening are considered in the following section.

### III. DEVELOPMENT OF DISPLAY COLOR.

**A. Sequence of Display Color Development.** In individuals as well as in the apparent trends of evolution within the genus, a certain sequence of chromatophoral display color development is discernible. This runs from black to red to yellow to white. When each of these colors appears dominant, obviously the pigment within the remaining chromatophores is concentrated. The full course of this black-white change is seldom run, and one or more phases are usually suppressed, but in various stages it can be traced in both groups of species and in individuals within a species. Also, save for some exceptions in the development of color on major chelipeds, the sequence never changes: for example, a white carapace never precedes a yellow, nor yellow legs red. Combination phases of orange, pink and cream in various stages of development occur frequently, however, and must be brought about by the simultaneous dispersal of red and yellow, red and white, and yellow and white pigment, respectively.

The fifth pigment, blue, which has been shown in other crustaceans to be extra-chromatophoric, is relatively uncommon and behaves irregularly. It is almost always confined to local areas, such as eyestalks, mouthparts or frontal regions. It may be said here only that it is a true display color, developing at the expense of diurnal black, and inhibited both by burrow submergence and

by capture. It seems always to develop before the general dispersal of white, and usually persists even when white has succeeded the remaining pigments. Often it has a strongly iridescent appearance, and may range in shade from purple and violet to turquoise and green, doubtless through simultaneous expansion of red or yellow chromatophores, respectively.

The behavior of the chromatophoric pigments will now be considered from other angles.

**B. Display White as an Evolutionary Trend.** In a previous paper (1941, p. 156) it was pointed out that dazzling white is exceedingly prevalent in the display coloration of the end-forms in each of the three groups of *Uca* in which display had at that time been observed. This white is assumed seasonally by the species, and daily by the individuals. Typical examples of this extreme whitening are *stylifera* in Group 1, *saltitanta* in Group 4 and *terpsichores* in Group 5. Since then, I have had opportunities of noting display coloration in a number of Group 2 fiddlers (examples: *pugnax*, *mordax*) as well as in other examples of the remaining groups, and have found no reason to alter the conclusion that the development of display-white is a general evolutionary trend throughout the genus. It is most common in the widely separated Groups 1 and 5, which contain the most specialized species, moderately so in Group 4, and rarest in Group 2; it is also well developed in 6, the offshoot proposed for the aberrant *panamensis* (*l.c.*, p. 166). Occurrence in Group 3 has not yet been studied.

Group 2 continues to appear to be the most primitive western hemisphere group, and, as just noted, white is less highly developed here than in any of the others. An exception is *galapagensis*, a close Pacific relative of *pugnax*; when seen in display, in Ecuador, 1944, the few waving examples were pure white; all the rest, both males and females, ranged from grayish to bright yellow and cream.

Depending on the sequence and extent of lightening of carapace in display coloration, species in which this phenomenon has been carefully observed may be divided into five divisions, as follows:

(a). Dark: No appreciable yellowing or whitening of carapace; display colors confined chiefly to appendages. Group 1: *maracoani*, *insignis*; Group 4: *oerstedii*, *spinicarpa*, *inaequalis*, *batuenta*, *cumulanta*.

(b). Carapace changes from dark to muddy yellow or grayish-white: Group 2: *pugnax*, *mordax*, *minax*; Group 4: *festae*.

(c). Carapace changes from dark to cream: Group 5 (primitive offshoot), *pugillator*.

(d). Carapace changes from dark to pink to white: Group 5, *stenodactyla* (but bright blue maintained anteriorly).

(e). Carapace changes from dark to yellow to cream to white: Group 1, *styliifera*, *princeps*; Group 2, *galapagensis*.

(f). Carapace changes from dark to cream to white: Group 4, *saltitanta*; Group 5, *beebei*, *deichmanni*, *terpsichores*, *latimanus*; Group 6, *panamensis*.

Several points must be emphasized here: First: the above represents *maximum* known color changes for each species. Sometimes, as in the case of *princeps* and *beebei* (see p. 166), they are not attained in every population. Sometimes, as in *pugnax*, dark displaying crabs are the rule, and lighter phases the exception. Contrariwise, individual crabs will be found displaying, or even actually mating, in colors not nearly as bright as those characterizing their immediate neighbors. Finally, (f) differs from (e) only in having the white pigment start diffusion simultaneously with, instead of subsequent to, the yellow.

Dispersal of red and yellow pigment often persists simultaneously with black, as may be seen by the persistence of red joints in *U. minax* apparently at all seasons, and of the frequent occurrence of reddish-or-yellowish-brown carapaces, as well as of ochraceous tinges on the chelipeds, even when some species are in their dark phases. Pure yellow and cream phases are exceedingly transitory, however, and require special comment. In at least the three species listed under (e) above, the adults, both males and females, of whole populations coming into the display season go for days, perhaps weeks, with daily changes to the bright yellow, or at most cream-yellow phase, but no continuation into white—that is, no subsequent concentration of yellow pigment accompanied by full dispersal of white. Later, individuals of *princeps* and *styliifera* have been seen to skip the yellow altogether in the daily change. Whether entire populations at the height of the breeding season may skip the yellow is not yet known. However, in the species listed under (f) above, which are preponderantly of the specialized Group 5, the creamy daily phase is sometimes so short as to be practically nonexistent, or it may be confined to some yellow speckles on the carapace, giving an over-all cream appearance.

To account for these phenomena, four separate chromatophoric actions must be explained, even when the frequent involvement of red and blue pigment is omitted: (1), The normal diurnal expansion of the black pigment is inhibited; (2), the yellow pigment is dispersed; (3), the yellow pigment is concentrated; (4), the white pig-

ment is dispersed. Whether a separate hormone is responsible for each mechanism is of course completely unknown. Equally unknown is whether these chromatophoral changes are merely by-products of physiological processes concerned in reproduction, whether they are a true adaptive result of display evolution, with recognition and/or stimulatory functions, or whether temporary intermediate phases, such as the yellow, are recapitulations of ancestral conditions. All three possibilities will probably be found to be true in part, and to vary with the species. Brown and Wulff's (1941, p. 344) observations on the behavior of yellow pigment in *Crago* should be kept in mind: the yellow in eyestalkless animals was first maximally concentrated and then rapidly dispersed by sinus gland extracts.

C. *Example of Color Development: U. princeps*. The large cheliped and often the ambulatories may run a course of color development independent of that of the carapace. For example, a majority of even the dullest fiddlers have the tips of the chelae completely white, and a great deal of red or orange at least on the major manus, while purple shades are common on the ambulatories. This red or orange sometimes persists even in species which otherwise change the carapace to complete white (example: *styliifera*). Again, the dispersed pigment of the cheliped may not only persist but may be white in the young, and reverse the usual sequence by developing orange and red secondarily, as shown below.

An example of ontological color development will be given in detail, as it occurs in *U. princeps*, which passes through a distinct yellow phase. The observations were all made at Puerto Bolivar, Ecuador, late in April. Apparently the display season was just beginning.

*Stage I.* up to ca. 10 mm. Carapace above and below greenish-brown; manus and chelae brilliant white, inside and out; ambulatories rich plumbaceous anteriorly; rest of cheliped and other legs muddy brown; eyestalks green or greenish-yellow. One exception, among hundreds of similar size, showed precocious coloration, being entirely white.

*Stage II.* ca. 11 to 18 mm. Like above, except for yellow developing on lower part of manus. This changes to dull orange, then blazing scarlet orange and spreads all over manus, inside of carpus and merus and throughout pollex except tip.

*Stage III.* ca. 19 mm. to maximum (ca. 30 mm.). Cheliped remains bright; carapace and legs lighten to dull orange.

*Stage IV.* Like above, except dull orange carapace and legs brighten to yellow, then cream. A few males in this stage fought and

displayed. This was the most abundant stage among adults, which obviously were not in full display season.

*Stage V.* Crab completely dazzling white except for bright orange pollex, or pollex and lower manus. All the males in this stage were displaying.

*D. Sexual Dimorphism:* As in many other groups of animals, there are species of *Uca* (e.g. *saltitanta*, *stenodactyla*, *latimanus*) where the female is always very dull and the male exceptionally brilliant in display coloration, while in closely related species the females are as bright as the males (except, of course, for absence of the often gaudily colored major cheliped). The latter group includes some species where white development reaches its height. The most striking examples of this found to date are the females of *princeps* and *terpsichores*, all observed in Ecuador. In others, such as *galapagensis* and *pugillator*, the female attains a cream only slightly deeper than the white or cream of the male. It may be noted that in species such as *stenodactyla*, where the female is very dull and the male especially bright, the dimorphism in size is also extreme; in those where the color difference is slight, the size difference also is relatively small. Here is another possible example of linked hormonal effects.

*E. Geographic Color Variation:* A most interesting observation made in Puerto Bolivar, Ecuador, gives evidence of marked geographic variation in the display colors of two species. Study of displaying *princeps* (Group 1) and *beebei* (Group 5) in Panama (February and March, 1941) during the dry season (1941, pp. 170, 193) showed that these species, although waving strongly, and with ovigerous specimens present, showed practically no white except on the fingers: instead, the display coloration consisted of gray, rose, orange and purple in *princeps* (which were in Stage II., p. 165), and gray, green, purple and ochre in *beebei*. Close relatives of each, on the other hand, *stylifera* and *terpsichores*, respectively, when in full display coloration had everything except the appendages dazzling white.

In observations made in April, 1944, at Puerto Bolivar, Ecuador, displaying individuals of both *princeps* and *beebei* were found to be almost completely dazzling white in color, although individuals of the darker and intermediate shades were present, as usual. In *princeps* there was also, as described above, an intermediate yellow phase. In *beebei*, a very few individuals in the darker phase characteristic of Panama were displaying; in *princeps*, none.

It was near the beginning of the dry season in Ecuador, so that the comparison with the Panamanian observations was

ideal. In morphological characters the individuals proved typical of their species in every detail, and their displays were indistinguishable. More evidence that the variation is actually geographic, and not a result of the observations of purely season differences, lies in the fact that immediately after the Ecuadorian study, the same Panamanian mud-flats at La Boca, Canal Zone, and Bellavista, Panama City, were visited during the second week in May, after the start of the rains. Both species were displaying, and both were in the identical dark coloration found three years previously during the dry, without a single white individual present, even on the clearest, sunniest days at full low tide.

A point of special interest concerns the size difference between displaying males of *princeps* in the two regions. In 1941 (p. 70) it was remarked that in the Panamanian colonies the largest males seen, all of which were displaying strongly, measured around 15 mm. in length, although the maximum measurements of specimens from other localities were around 25 mm. In addition, it has been determined that in these small males the abdominal appendage is slightly pre-adult in form. The same conditions prevailed there in 1944 in the colony at Puerto Bolivar; however, the only males displaying were large individuals measuring around 25 to 30 mm., with abdominal appendages of mature development, and all of these were in the white, or at least the creamy-yellow phase. As far as could be determined, general ecologic factors were exceedingly similar; in both the Panamanian and Puerto Bolivar populations, the salinity (high tide, near full moon: unfortunately only one sample was taken from each) was about 38 parts per thousand, or about 75 per cent. of average open ocean concentrations; also, the general facies of the mud-flats, including high Pacific tides, and climatic conditions with pronounced wet and dry seasons, were much alike.

There are at least four possible explanations, which are not necessarily mutually exclusive.

(1). In the Panamanian habitat some unknown environmental factor may promote early maturation of the sex glands before maximum size and pigment development are attained.

(2). Contrariwise, a factor may inhibit development of the last two characteristics.

(3). In Puerto Bolivar, some factor may encourage the production of white and yellow pigment, or of the hormone(s) governing their dispersal, or both. Since the white is confined to displaying forms, however, connection with gonad activity still seems essential. Also, this alternative would not



be adequate to explain the small size and pre-adult form of abdominal appendages in Panamanian *princeps*. It would however be sufficient to cover the development of the white in Ecuadorian *beebei*, which show no size or appendage difference from Panamanian specimens.

(4). A fourth explanation, which would apply equally well to both species, is that in Puerto Bolivar species development, through mutation and selection, has progressed beyond the stage found at Panama, and has reached the normal summit of *Uca* color evolution, which tends toward white display dress in all groups.

Because of the lack of morphological differences and the presence of Panamanian color phases in both *princeps* and *beebei* at Puerto Bolivar among the white individuals, there seems to be no adequate basis at present for the erection of subspecies or other subdivisions. The same two species must obviously be studied in other localities and at all seasons before the "normal" forms can be identified.

**F. Ecologic Factors:** Too little is known of precise ecological factors to draw any conclusions at present. It may only be stated here that so far as known crabs with the most brilliant coloring, including development of display white, live only on tropical shores with more than half the salt concentration of open ocean water and a high tidal range. In the western hemisphere, these conditions are met in the tropical eastern Pacific, where the most active species, and the greatest numbers of species also occur. Second, bright sun is needed to bring about maximum dispersal of white pigment, just as it is necessary for maximum display activity: although there are always individual exceptions, a given population is invariably notably darker and far less active on cloudy days than on clear.

#### IV. SUMMARY AND CONCLUSIONS.

Four types of normal color changes in *Uca* have been described, namely diurnal darkening, submergence darkening, darkening on capture and display brightening. None except the first has been studied microscopically or investigated experimentally from an endocrinal viewpoint. It is already fairly certain that diurnal darkening is brought about by a secretion from the central nervous organs; it is suggested in the present paper that the slow-working submergence darkening may be motivated by the dark-dispersing element of the sinus gland, while the relatively rapid darkening on capture may be controlled by the latter, or by another element in the nervous organs. The display brightening

principle(s) inhibit the diurnal darkening mechanism as well as the normal sinus gland darkening, and are in turn inhibited by those of the submergence and capture darkening.

Display brightening includes, in addition to widely occurring bright chelipeds and ambulatories in males, a general trend throughout the genus toward the development of complete dazzling whiteness in both sexes during the display season. Fully white crabs occur in widely separated species. In ontological seasonal and daily changes, a strict sequence of display color development is apparent, which runs from black to red to yellow to white, each phase representing dispersal of one of the four chromatophoric pigments. Any of the phases except the first may be suppressed, and combinations are frequent, giving orange, pink and cream effects. Yellow and cream phases are the most transitory. In most but not all species where bright display color is well developed, the carapaces of the females are decidedly darker than those of the males. Two cases of geographic color variation are described, where displaying males of two unrelated species are dazzling white in Ecuador and much darker in Panama, under apparently similar ecological conditions. In one species, the dark Panamanian examples, although giving all signs of actual breeding, were in addition small with subadult abdominal appendages.

Ecologic factors for development of display color have not yet been specifically studied. Bright sun, however, is essential for maximum daily development of display color. So far, the brightest and most active of western hemisphere species, as well as the greatest local concentration of species, have been observed in the tropical eastern Pacific on shores with high tidal ranges and with a salinity concentration of more than half that of open ocean water.

The above data has been put on record with the chief hope of suggesting lines for future endocrine and psychological research in this group, preferably with a combination of field and laboratory methods. The adaptive functions of display color are still only suspected: it is not even known whether fiddler crabs have color vision, much less whether the brightening of the male crab in display has recognition and/or stimulating value for the female, and serves for territorial limitation and challenge to other males, whether it is merely a metabolic by-product, or whether recapitulation of ancestral color is involved in cases of transitory phases. Judging from the behavior of the females and rival males, however, it seems certain that at least the brightness (irrespective of color) of the waving chelae,

which adds so much to the conspicuousness of the display in even the dullest species, must be of actual value.

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## 16.

## Anatomy of the South American Woolly Monkey (*Lagothrix*). Part 1. The Forelimb.

DONALD FORD ROBERTSON, M. D.

(Plates I-V).

### INTRODUCTION.

In presenting this description of the gross anatomy of the forelimb of *Lagothrix*, the South American woolly monkey, it should be explained that subsequent papers are planned to cover the entire body. These will consist of appropriate regional divisions, designed, so far as possible, to permit ready integration.

Rather than employing the standard, systematic method, I have chosen the regional or "dissector's manual" type of description. In my opinion this is the only logical way to present the material in a form that is readily usable for practical purposes. Functional interpretations will be omitted except in those parts where the anatomical details revealed in the dissection seem to lend themselves particularly to the emphasis of certain points, or where the functional aspect appears to require an especial annotation underlining the conclusions I have reached.

The anatomical material on which this description is based consists of one adult female, one young female, and one male infant. The first two are *L. lagotricha*, the third *L. cana*. I am indebted to Dr. L. J. Goss, veterinarian of the New York Zoological Park, for his great courtesy and generosity in placing this material at my disposal. Without his help and encouragement much of this work would not have been possible.

A search of the literature has revealed only the most fragmentary data on the genus *Lagothrix*.

I am indebted to Dr. R. J. Terry, Professor of Anatomy, Washington University, School of Medicine, and Dr. M. J. Guthrie, Professor of Zoology, University of Missouri, for their kindness in reading and correcting the manuscript.

### EXTERNAL CHARACTERISTICS.

The upper extremity in *Lagothrix*, as in all primates, is a remarkably differentiated member capable of a great variety of movements and serving for locomotion, and in

particular, prehension which is characteristic of primates. By grasping objects and drawing them near for close visual inspection, and for stereognostic appreciation, the primate is peculiarly favored in a minute and accurate orientation to its environment.

The upper extremity of *Lagothrix* acts simply as a forelimb when the animal is walking on the ground. The hand, with its characteristic position of flexion into a balled fist, carries the weight on the well-developed hypothenar eminence which presents a proximal extension. The flexed fingers may bear some weight as would the toes for very brief periods in man, but the fingers are never extended while the animal is walking on a flat surface, and any weight-bearing by the fingers is on the dorsal surface of the distal phalanges of the flexed digits. This is of interest as it may represent a stage in the development of the digital posture of the anthropoid hand.

*Lagothrix* is not usually thought to be a brachiator, but some authors have mentioned observations of the occasional use of this method of progression. I have frequently observed genuine brachiation, although it must be admitted that it is modified by the constant use of the prehensile tail for temporary support as well as maintenance of balance. This is in contrast to *Ateles* which frequently brachiates without employing its tail for support, and of course to the anthropoid apes which lack a tail. The forelimb is very important in climbing and in supporting its share of the weight in the four-legged type of progression erect or inverted.

The hand presents its most specialized prehensile activities, however, when the position of the animal, such as sitting on its haunches, standing erect on the hinder extremities, or hanging supported by them and the tail, frees the arms for this purpose. The grasp, as discussed elsewhere, is of two general kinds—one a simple haphazard and hasty grasp, the other more elaborate and directed toward exact approach to the object.

### Integument.

The skin of the forelimb is thickly covered with the thick rabbit fur-like hair characteristic of this genus for which the name was given. As a general rule, all species or types show a tendency to a predominance of darker hair from the elbows distally. The hair is dense on the extensor surfaces. It is thinner and sparse on the flexor surfaces, presenting bare spaces in the axillae about the nipple, in the supraclavicular region and in the antecubital fossa. Elsewhere it is thick and dense. Adults of all types present along the anterior border of the limb a thick fringe of long hair, often of great length. On viewing the animal anteriorly, this is seen to be the upper arm of a chiasmal growth that runs down the mid-ventral region and extends along the upper and lower extremities at the cephalic borders. The skin is everywhere freely movable. It is thin and less elastic on the flexor surfaces and thicker and more turgid on the extensor aspect.

The integument of the palm displays the characteristic ridges and grooves, assembled in configurational systems, comprising the patterns of the volar pads and the intermediate and surrounding areas in which there is no definitive arrangement. The variability and diversity of pattern configuration and distribution is such that, like man, no two individuals present identical arrangements. In some twelve pairs of hands I have thus far examined, no repetitions have been found.

The generalized plan of volar pads, as exemplified by the chiroidia of the lower mammals, has been materially modified, although remnants of each of the general classifications described by Whipple (4) may be found, varying from one individual to another. The apical pads on the tips of the fingers are comparatively constant and show a monotonous similarity of concentric rings, varying to some degree in the minutiae. Pads on the middle and proximal phalanx show a somewhat greater degree of diversity and variation although they too present little of the specialized diversifications of the palmar pads proper. If one can accept the thesis that the elaboration of the patterns is correlated in some degree with the role of these areas in tactile sensibility and hence with perceptual accuracy, it is suggested that the palmar surface of the proximal phalanges and the opposing surface of the palm constitute the chief areas of perception in this monkey. The interdigital pads in the hands examined are occasionally absent, or much reduced (one specimen), but in all the others there were at least two and in some cases three. These consist of numbers I

and II and occasionally III (Whipple's generalized schema). In both hands of one specimen there are intermediate pads with patterns of concentric rings. These are sufficiently well organized and discrete to be considered as probably independent developments and not due to segregation by the superimposed creases, of areas formerly included with the interdigital pads. The thenar and hypothelar areas present well-developed pads, although in none of the specimens I have examined do these pads present significant arrangement of ridges and sulci into concentric rings or whorl-like patterns. They consist, then, simply of open fields, but contrary to the statement of Bychowska, (2) I do not find, except in one specimen, that the lines are directed proximo-distally; on the contrary the direction in all cases is from side to side. This might be expected in view of the importance of these areas, especially the large hypothelar pad, in weight bearing when the animal walks on all fours. The transverse direction naturally increases the frictional resistance, also thought to be an important function of these ridges by some observers. I do not find the areas on the palmar surface proper in which epidermic warts rather than ridges are found by Whipple. In all my specimens the intervening areas between patterns are covered by skin bearing well-developed ridges and at the margins of the palmar area, the ridges simply fade out into non-sculptured skin with no transition in the form of wart-like structures.

The hand of *Lagothrix* has been well described by Pocock (5) as *zygodactylous*. That is, the space between digits two and three is much wider than that between one and two, and the grasp, especially of small elongated objects, is between digits two and three. The thumb should not be disregarded in this connection, however, since, while it moves with the index and the two digits constitute what I call the "thumb unit," it is capable of a considerable degree of independent motility, especially when the index is fixed. There appear to be two possible explanations for this development of a thumb unit consisting of digits one and two; first, that this zygodactylous separation is directed by the same forces that have determined the development or persistence of the cloven hoof of digitigrade quadrupeds; or, second, that this functional division simply represents an individual specialization emphasizing the importance of the index in the absence of independent functional potentialities of the pollex which is incapable of opposition, and is here simply a satellite of the index. It must be considered also that a combination of factors is operative here since in these monkeys

the hand serves a dual function, that of support in the suspended position or in walking on all fours, and also serves to grasp movable objects of various sizes. In the one case strength and stability of structure are essential, while in the other delicacy of motion with graded approaches and refinements of manipulative power are required. At this stage I am not prepared to discuss the importance of the respective factors.

#### *Subcutaneous Tissues and Cutaneous Nerves—Fasciae.*

On removing the skin the loose areolar tissue forming the superficial fascia is revealed. There is rarely an appreciable amount of fatty tissue, hence care must be exercised in removing the skin to preserve the superficial sensory nerves. Except for the area of their terminal distribution these run beneath the deep fascia. The deep fascia is not so well defined as it is over the forearm structures. This is especially true around the shoulder region and the upper part of the arm. About the elbow and from there distally, however, the deep fascia forms a well-defined sheet of considerable strength.

The *Nn. supraclaviculares* will be described in detail with the cervical plexus. Two of these emerge in the region of the acromion to supply the skin of the supraclavicular fossa and the superior aspect of the shoulder. The anterior aspect of the shoulder over the deltoid muscle is supplied by a branch of the *N. dorsalis scapulae* that emerges between the deltoid and pectoralis major in the groove containing the cephalic vein. The medial aspect of the arm is supplied by the medial brachial cutaneous nerve whose rami perforate the deep fascia serially. The branches of the medial antibrachial cutaneous nerves spread out in fan-shaped manner over a triangular area on the medial aspect of the forearm, the most distal continuing almost to the wrist. The intermediate antibrachial cutaneous nerves may be more conveniently described later. The lateral brachial branches of the *N. radialis* emerge in the lower half of the arm in the region of the lateral intermuscular septum. These branches supply the lateral aspect of the lower third of the arm and the elbow region. The lateral antibrachial cutaneous nerve consists of three branches supplying an elongated triangular area of the lateral and dorsal aspect of the forearm. The posterior aspect of the shoulder and arm are supplied by cutaneous branches of the *N. axillaris* which emerge from the lower border of the spinous division of the *M. deltoideus*.

The superficial veins of the hand and forearm form two main trunks, the cephal-

ic and basilic, which are formed on the lateral and medial aspects of the wrist by the union of variable veins draining the fingers and dorsum of the hand. There is no dorsal arch and these venous channels from the hand arise from the first and second and from the fifth digits only. The cephalic vein passes upward along the dorsolateral aspect of the forearm and the arm passing medially over the superior border of the *M. pectoralis major* and behind its clavicular origin to join the *Vv. brachiales*. The basilic vein passes upward over the medial and volar aspect of the arm to the antecubital fossa where it pierces the fascia to join the *Vv. brachiales* at this point.

#### *Anterior Thoracic Region.*

The fascia of the anterior thoracic region is irregular in thickness, being less restrictive over the main area of the pectoral region. It becomes better defined near the lateral margin of the *M. pectoralis major* at its lower border. This fascia forms a definite diaphragm between the *M. latissimus dorsi*, the *M. pectoralis major* and the fascia of the arm in the axilla. On each side of the midline the fascia is pierced serially by the anterior cutaneous branches of the intercostal nerves, and in the mid-axillary line by their lateral divisions. The fascia is attached firmly to the clavical superiorly and along a median raphe the entire length of the sternum.

The *M. pectoralis major* arises, as in other monkeys, from a median raphe with interlacing fibers crossing the midline from the entire length of the manubrium and corpus sterni, the sternoclavicular joint and the medial third of the clavicle. The upper margin of the lateral third of the pectoralis major lies beneath the lower margin of the deltoid. On separating the deltoid from the pectoralis major the origin of the latter from the inner third of the clavicle and the course of these superior fibers which insert at the lowest point on the humerus are better revealed. When the pectoralis major is severed from its sternal origin and reflected, the inferior portion is found to arise in two sheets, the superficial from the sternum and median abdominal raphe, the deep from the costal cartilage of the sixth rib. These lower fibers take a progressively deeper position as they proceed to the insertion at the highest point on the lateral lip of the bicipital groove of the humerus. When the pectoralis major is turned upward the anterior thoracic nerves and an artery are seen entering its deep surface. This neurovascular bundle passes between the pectoralis minor and the pectoralis abdominis.

A small accessory pectoral muscle which

may be called the *M. pectoralis accessorius* in the absence of other identification, has been found in these specimens. It arises variably from the deep fascia of the abdomen or from the sixth or seventh rib lateral to the lower border of the pectoralis major, and passes behind the major in the midclavicular line to insert with it by a fine aponeurotic tendon on the under surface of the pectoralis tendon. Its functional significance is obscure. A fine branch of the anterior thoracic nerve passes downward to it from the rami supplying the pectoralis major.<sup>1</sup>

The *M. pectoralis minor* arises superficially from the costal cartilages of the third, fourth and fifth ribs, the individual parts being separated by perforating branches of the intercostal arteries and nerves. On reflecting this superficial sheet a deep origin is revealed. This is formed by separate slips of aponeurotic structure from the third, fourth and fifth costal cartilages at a point lateral to the origins of the superficial sheet. There is a third and still deeper origin from the costal cartilage of the second rib. These three sheets are easily separable up to their point of fusion, just short of the insertion by an aponeurotic tendon which the *M. pectoralis minor* shares with the pectoralis abdominis, covering and attaching to the lesser tuberosity of the humerus. The pectoralis minor is supplied by its own artery and nerve from the anterior thoracic and thoracoacromial group.

The *M. pectoralis abdominis* arises by both a deep and a superficial head. The former lies directly under the latter as they arise from the seventh rib and from the sheath of the rectus abdominis. At mid distance from their origin these two heads diverge, the superficial being inserted more distally than the deep, which occupies an intermediate position between the former and the pectoralis minor, on a thin common tendon of insertion. This covers the lesser tuberosity of the humerus, lying superficial to the insertion of the subscapularis.

When the superior and deep head of the pectoralis minor are reflected, the origin of the subclavius muscle on the costal cartilage of the first rib is revealed. Lateral to the origin of the subclavius is found the upper head of a segmented muscle arising from the first, second, third and fourth ribs in the midclavicular line, each slip giving rise to a thin, flat aponeurosis superimposed one on the other to fuse with the origins of the pectoralis minor on the costal cartilage of the fifth

rib. Beneath its termination the uppermost origin of the rectus abdominis from the fourth costal cartilage can be seen. This muscle is only revealed in its full extent in the dissection of the thoracic wall and will receive further consideration in that section.

Separation of the anterior margin of the deltoid from the pectoralis major reveals that, except for about a centimeter of its length, the insertion of the pectoralis major is covered by the deltoid. The two muscles diverge near the clavicle and a bare area of this bone in its middle third is revealed.

The *M. deltoideus* has a lengthy linear origin, and according to the various points may be divided into clavicular, acromial and scapular (spinous) parts. The clavicular origin is from the lateral third of this bone, separated by a distinct interval from the clavicular origin of the pectoralis major. This hiatus of the muscles leaves the bare area described above. The clavicular fibers sweep downward over the insertion of the pectoralis major, with the deeper fibers forming an aponeurotic tendon which fuses in part with the tendon of the pectoralis major. The acromial origin occupies the full curve of this prominence, and these fibers proceed straight downward to insert on the lowest point of the deltoid crest of the humerus. The scapular origin consists of a thin triangular sheet with a concave lower margin arising in part from the lateral two-thirds of the inferior margin of the spine of the scapula and in part by a thin membranous aponeurosis from the lower third of the vertebral margin of the scapula. These lower fibers sweep laterally and converge downward to join the acromial division, inserting posteriorly on the humerus. The deltoid is supplied by the *N. axillaris* which is spread over its deep surface in fan-shaped manner. The nerve is accompanied by the terminal muscular branches of the posterior circumflex humeral artery.

If the deltoid is severed near its origin and reflected downward, the insertion of the pectoralis major is found to fuse in part with the insertion of the anterior fibers of the deltoid. The superior portion of this conjoint tendon forms a tunnel through which the tendon of the long head of the biceps passes from its intra-articular origin to insert on the supraglenoid tubercle.

The axillary fossa is pyramidal in shape with the base presenting laterally. The pectoral muscles together with the common origin of the coracobrachialis and the short head of the biceps form the anterior covering of the fossa. Posteriorly it is bounded by the *M. subscapularis*,

<sup>1</sup> THIS muscle may be the sole persistent representation of the *M. panniculus carnosus*. Its insertion with the pectoralis major speaks for this explanation (see Hartman & Straus, p. 103), although its origin suggests that it is a part of the pectoralis complex.



medially by the chest wall, and laterally by the axillary fascia. On removing the axillary fascia and the pectoral muscles the axillary neurovascular bundle is revealed. The first third of the axillary artery is bounded below by the axillary vein and posteriorly by the combined cords of the brachial plexus. The middle third of the artery lies behind the cords of the plexus and continues in this position in its distal third. The axillary vein lies first below the artery and nerves and then passes behind the nerves to occupy a position medial to the axillary artery just before it becomes the brachial artery. The first branch of the axillary artery in the axilla is the *A. thoracoacromialis*. This divides into pectoral branches to the *Mm. pectoralis major*, minor and abdominis, and gives deltoid and acromial branches to the clavicular and acromial origins of the deltoid. Proximal to the origin of thoracoacromial artery, the medial cord of the brachial plexus gives off muscular branches to the pectoral group and to the subclavius. From the thoracoacromial trunk three arteries constitute its terminal branches; these are the *A. thoracalis suprema*, the *A. thoracalis lateralis* to the serratus anterior, and the *A. thoracodorsalis* supplying the latissimus dorsi. The latter is accompanied by the *N. thoracodorsalis*. The long thoracic nerve passes to the serratus anterior somewhat posterior to the region of the muscle to which the *A. thoracalis lateralis* is supplied. *Note:* To display the brachial plexus in its entire extent it is necessary to disarticulate the clavicle from its sternal attachment and reflect certain structures having attachments in this region. Since this necessitates disturbing these parts, they will be described here.

The *M. sternocleidomastoideus* separates into two distinct bellies in the lower part of the neck. The lateral one inserts on the upper and posterior surface of the medial third of the clavicle. The medial head passes anterior to the sternoclavicular joint and inserts on the superior and anterior aspect of the manubrium sterni posterior to the upper fibers of origin of the pectoralis major. When the lateral head of the sternocleidomastoid is reflected from its clavicular insertion the sternoclavicular joint is revealed.

The *articulatio sternoclavicularis* is a typical diarthrosis with an articular disc of fibro-cartilage. The capsule is loose and permits comparatively free movement. The ligaments consist of the anterior and posterior sternoclavicular ligaments passing in an oblique manner laterally from the sternum. The posterior is several times stouter than the anterior ligament. There is also a costoclavicular ligament between

the clavicle just distal to the joint and the superior margin of the first costal cartilage.

By severing the ligaments and releasing the joint, and by severing the *M. subclavius* just beyond its stout origin on the anterior surface of the first costal cartilage and superior surface of the first rib, the clavicle may be displaced and the entire brachial plexus is revealed. Passing over the superior belly of the *M. sternocostalis* is the axillary vein and above it is the axillary artery, lying here on the insertion of the *M. scalenus anterior*. Here the axillary also comes into relation with the upper surface of the arch of the first rib. Prominent in this region is the *V. jugularis externa* passing downward to join the *V. jugularis interna*. The *N. phrenicus* crosses over the subclavian artery to enter the mediastinum just lateral to the *A. cervicalis ascendens*. This latter divides into the *A. transversa scapulae* and continues on as the ascending cervical. The transverse scapular artery gives a branch to the lateral head of the *M. sternocleidomastoideus*, and then passes posteriorly to the superior border of the scapula where it divides into superficial and deep branches. Its further course will be described with that region.

The *M. subclavius* is a very stout muscle in *Lagothrix*. It passes upward and laterally from its origin on the costal cartilage of the first rib, behind the clavicle, to insert on the postero-inferior surface of that bone near the attachment of the acromio-clavicular ligament. A second part of the muscle diverges and passing posteriorly inserts on the superior border of the scapula near the base of the coracoid process.

#### *The Brachial Plexus.*

The fifth, sixth, seventh, and eighth cervical and the first thoracic nerves form the brachial plexus. These divide into anterior and posterior divisions, which in turn form the lateral, medial and posterior cords by reunion. Union of the anterior divisions of the fifth and sixth nerves forms the lateral cord, while the medial cord is formed by the union of the anterior divisions of the seventh and eighth nerves, and the posterior cord by the union of the posterior divisions of the fifth, sixth, seventh and eighth nerves. The fourth cervical nerve contributes to the brachial plexus solely by the branch which joins the rami of the fifth and sixth nerves to form the *N. phrenicus*.

The first branch of the lateral cord is the *N. suprascapularis* which consists of the major part of the fibers of the fifth cervical nerve. This passes laterally and posteriorly over the superior margin of

the scapula medial to the insertion of the *M. subclavius* and beneath the *M. supra-spinatus*.

Next the lateral cord gives off in succession the ramus of the fifth cervical root to the *N. phrenicus*, and a ramus which joins with a branch of one from the medial cord to form the anterior thoracic nerve to the pectoralis major; the second branch of this ramus from the medial cord passes to the pectoralis minor.

Soon the lateral cord terminates in the *N. musculocutaneus* and in the lateral head of the *N. medianus*. In some specimens this lateral head may receive a contribution from the medial cord before the junction of the medial head itself.

The medial cord may consist of a well-fused mass from the anterior divisions of the seventh and eighth nerves, or these two may combine only at a point somewhat proximal to the formation of the medial head of the *N. medianus*. In the latter case it is clear that the contribution to the anterior thoracic nerves comes from the eighth cervical and that the latter also gives off the medial brachial cutaneous, the medial antibrachial cutaneous, and the intermediate antibrachial cutaneous nerves. The terminal branches of the medial cord are the medial head of the *N. medianus* and the *N. ulnaris*.

The posterior cord like the median cord may form a group of loosely joined plexiform branches with only a small part of its extent forming a true cord. It must be admitted that the separation effected by dissection is often artificial, but it serves to define more accurately the representation of the cervical segments in the final common pathway. The first branch of the posterior cord is the *N. thoracalis lateralis* which arises from the sixth cervical nerve near its spinal exit, and passes inferiorly through some of the heads of origin of the *M. scalenus anterior* to emerge near the anterior border of this muscle and pass obliquely downward and posteriorly over the *M. serratus anterior*, terminating in its individual heads by segmental branches.

The posterior cord gives off a series of subscapular branches to the muscle of that name. Those supplying the more posterior heads come from the fifth cervical, the next from the sixth, while those nearest the anterior border of the scapula are clearly derived from the seventh cervical nerve.

The *N. axillaris* is formed by the posterior divisions of the fifth, sixth, and seventh cervical nerves. The remaining branches of the various contributions enter into the formation of the *N. radialis*. From the medial (eighth cervical) contribution, the *N. thoracodorsalis* to the *M.*

*latissimus dorsi* passes downward and laterally to distribute itself over the inner surface of the muscle. Near its exit from the axilla, the *N. radialis* gives off the muscular branch to the epitrochlearis and a ramus which joins the ulnar nerve and passes distally in its sheath to the mid portion of the arm where it passes to the deep-lying medial head of the triceps.

On the right side the fifth cervical nerve contributes to the phrenic nerve with a ramus as large as that forming its source from the fourth cervical nerve. The ramus from the fifth receives a slender branch from the cervical sympathetic trunk and in addition gives off the motor branch to the *M. subclavius*. It then curves anteriorly over the *M. scalenus anterior* to join the phrenic trunk.

On the left side the phrenic nerve receives contributions from the fifth and sixth cervical nerves as well as from the fourth. The nerve to the subclavius likewise arises on the left side from the fifth cervical root of the phrenic nerve.

Returning to structures about the shoulder joint, anteriorly the common origins of the *Mm. coracobrachialis* and *biceps brachii, caput breve*, superimposed on each other, form a stout tendinous band passing obliquely into the medial aspect of the arm. When this common tendon is severed and reflected, the *N. musculocutaneus* is found along the posterior surface, giving branches to the *M. coracobrachialis* in this region. From the deep surface of the coracoid process beneath the *M. coracobrachialis*, a thin, flat muscle arises and passes laterally to insert on the antero-medial surface of the neck of the humerus just above the insertion of the *latissimus dorsi* on the medial lip of the bicipital groove. This muscle is supplied by a slender branch of the anterior humeral circumflex artery, which curves laterally below its insertion, and it is innervated by a branch of the musculocutaneous nerve. Hartman & Straus (7) call this muscle the *M. coracobrachialis profunda* in the rhesus monkey but its separate and distinct course in my opinion makes it worthy of distinctive designation. I have called it the *M. coracohumeralis*.

In the region about the shoulder joint the combined tendon of the *latissimus dorsi* and dorso-epitrochlear muscles lies distally and deep to the coracobrachialis. These two muscles join at an acute angle in the posterior part of the axilla to form the broad, flat tendon which inserts on the superior part of the medial lip of the bicipital groove anterior to the insertion of the *teres major*. The latter occupies a position posterior to the former along the entire length of the medial lip. Between these tendons there is a large bursa.

In the bicipital groove the prominent rounded tendon of the long head of the biceps is seen passing inferiorly to pierce the capsule of the shoulder joint from its origin on the supraglenoid tubercle. When the short head of the biceps is reflected with the coracobrachialis the origin of the anterior humeral circumflex artery is revealed arising from the axillary artery near the inferior border of the coracobrachialis. It passes beneath this muscle and the musculocutaneous nerve to give branches to the distal part of the pectoralis major and to the *M. coracobrachialis*. A recurrent branch passes to the subdeltoid area of the capsule of the shoulder joint and anastomoses with branches of the posterior humeral circumflex and acromial branches of the thoracoacromial arteries.

The pectoral group of muscles is evidently quite variable and inconsistent. In a full grown female (*L. lagotricha*) the pectoralis major arises from the inner third of the clavicle, from the sternum down to the end of the gladiolus and from the seventh costal cartilage. There are no fibers extending from the sheath of the rectus abdominis. The accessory pectoral muscle arises by two heads from the sixth and seventh costal cartilages, the superficial somewhat lateral to the deep head. The two combine near their mid portions and become narrow and rounded. Beyond this point the muscle becomes flattened and fan-shaped. It passes behind the lower border of the pectoralis major and the fan-shaped insertion joins with that of the latter near its superior part. The pectoralis minor arises from inferior, deep and superficial heads. The first takes origin from the sixth costal cartilage. The latter two from the third, fourth, fifth and sixth costal cartilages. All of these join to insert in a common tendon on the lesser tuberosity. In this specimen there is no muscle which can properly be identified as the pectoralis abdominis.

#### Posterior Thoracic Region.

The *M. atlantoscapularis superficialis* runs obliquely from the atlas to insert on the lateral extremity of the spine of the scapula near the base of the acromion and covers the acromial insertion of the trapezius.

The *M. trapezius* has a broad transverse origin from a horizontal line on the occipital bone and from the spinous processes of cervical vertebrae by direct, fleshy bundles. At the level of the lower cervical vertebrae the muscle bellies retreat laterally, giving place to a triangular aponeurosis which extends down to about the fourth thoracic vertebra. From that point to the end it arises again directly from the vertebral spines and interspinous ligaments. The cervical portion is inserted on the superior

surface of the outer third of the clavicle, on the acromion, and the entire length of the scapular spine. The lower portion inserts only on the inferior margin of the medial third of the scapular spine.

Inferior to the trapezius the posterior attachments of the deltoid are observed to consist of the posterior part of the acromial section and the spinal division which have been described.

On reflecting the trapezius from the vertebral origins the *M. rhomboideus capitis* is revealed. This muscle originates by two heads. The medial head arises from the occipital bone below the origin of the trapezius and from the nuchal ligament, while the lateral head arises by a fan-shaped origin from the occipital bone beneath the origin of the trapezius. These two heads merge to form a wedge-shaped muscle which inserts on the upper third of the vertebral margin of the scapula near the superior angle.

The *M. rhomboideus cervicis* arises from the spines of the cervical vertebrae and is inserted along the vertebral margin of the scapula just inferior to the insertion of the *rhomboideus capitis*.

The *M. rhomboideus dorsi* arises from the first four or five thoracic spines and is inserted along the vertebral margin of the scapula down to the inferior angle.

The *M. atlantoscapularis posterior* which is revealed on a deeper plane when the trapezius is reflected laterally, arises from the transverse process of the atlas and passes downward and posteriorly to insert on the posterior superior scapular angle, lateral to the insertion of the *rhomboideus capitis*.

When the fat, areolar tissue and the deep chain of cervical lymph nodes are removed from beneath the trapezius, the *A. transversa scapulae* is observed passing posteriorly and laterally. After crossing the superior margin of the scapula the artery gives off a long muscular branch to the trapezius and a superficial and deep branch to the *M. supraspinatus*. There is also a contribution to the periarticular anastomotic rete over the shoulder joint.

The reflection of the trapezius reveals the origin and main body of the *M. supraspinatus* which takes origin from and occupies the entire supraspinous fossa. Crossing its surface is the superficial branch of the transverse scapular artery which gives off muscular branches here and continues downward to anastomose with the terminal branches of the posterior circumflex humeral artery. The deep branch of this artery passes beneath the supraspinatus, emerging at its lower border beneath the coracoclavicular ligament to contribute its acromial branches to the rete acromiale. From there

the artery continues on as the *A. transversa scapulae profunda* beneath the root of the acromion, where it enters the infraspinous fossa to supply the *M. infraspinatus* and the *M. teres minor*. It is accompanied by the *N. dorsalis scapulae* which supplies the *Mm. supraspinatus* and *infraspinatus*. The *M. teres minor* is supplied by the *N. axillaris*. This ramus enters the muscle near its insertion. The *M. supraspinatus* forms a well-defined tendon which inserts at the highest point on the greater tuberosity of the humerus.

In the infraspinous fossa lie the bellies of the *M. infraspinatus* and the *M. teres minor*. Passing over them superficially is the aponeurotic (origin of the long head of the *M. triceps*) from the spine of the scapula. Medial to the long head of the triceps, the terminal muscular branches of the posterior humeral circumflex artery emerge from between the teres major and minor, ending in the teres major, minor, and infraspinatus. Lateral to the long head of the triceps, the deltoid branches of the posterior circumflex artery emerge with the axillary nerve.

By reflecting the latissimus dorsi, after severing it near its insertion, the inferior angle of the scapula is revealed. Three muscles converge here: The teres major arises from this angle and the entire length of the axillary margin of the scapula. The lower bellies of the *M. serratus anterior* insert on the inferior angle. The lower fibers of the *M. rhomboides dorsi* from the mid-thoracic spines pass superiorly to insert near the angle.

The major part of the infraspinous fossa is occupied by the *M. infraspinatus* but it shares this area with the *M. teres minor*. The latter is flattened from above downward near its origin, but becomes flattened from before backward so that the fibers having the deepest origin are inserted at a higher point on the greater tuberosity. This insertion is directly below that of the *M. infraspinatus*.

When the rhomboid muscles are severed from their origins and reflected, the descending branch of the transverse scapular artery is found passing downward on the deep surfaces of the rhomboideus capitis and cervicis. The artery continues its course inferiorly and contributes to the anastomoses along the vertebral margin of the scapula.

The *M. splenius capitis* arises from the external occipital protuberance and nuchal ligament to the first or second thoracic spine. Overlying the lower part of this origin is the thin aponeurotic sheet of origin of the serratus posterior superior. Fleishy muscle bundles of the latter, three or four in number, appear beyond the margin of the epaxial musculature and insert on the corresponding ribs. The insertion of the splenius

capitis is on the superior nuchal line laterally as far as the mastoid process.

There is a prominent representation of the levator scapulae complex which arises from the transverse processes of the cervical vertebrae and inserts on the superior margin of the scapula to the superior angle, occupying a space between the insertion of the *M. atlantoscapularis posterior* and the upper insertion of the *M. serratus anterior* and *M. rhomboideus capitis*.

#### *Medial and Anterior Aspect of the Arm.*

As the deep fascia is removed, the branches of the medial brachial cutaneous and medial antibrachial cutaneous nerves are revealed. The latter continues downward in the groove between the biceps and dorso-epitrochlearis to emerge near the antecubital fossa. These have been observed in the axillary fossa arising by a common trunk with the anterior thoracic nerves from the medial cord of the plexus. The intermediate antibrachial cutaneous nerve, also a branch of the medial cord, runs along the medial border of the short head of the biceps, crosses under the lacertus fibrosus and continues down the middle of the volar surface of the forearm to the wrist.

When the short head of the biceps is separated from the dorso-epitrochlearis and reflected laterally, the neurovascular bundle of the arm is exposed. The *A. brachialis* occupies the following positions with respect to the median nerve which may be taken as a point of reference: The artery and vein lie lateral to the median nerve in the upper third of the arm. At its middle third the artery passes behind the nerve. Just before this occurs the *A. profunda brachii* arises and passes posteriorly in company with the *N. radialis*. The latter has occupied a position posterior to the artery up to this point. The *A. nutricia humeri* arises from the *A. brachii* in its upper third just below the *A. profunda brachii*. The brachial artery in the lower third of the arm lies medial to the median nerve and posterior to the brachial vein. In the arm the brachial artery gives off muscular branches to the long and short heads of the biceps, to the brachialis, the *A. profunda brachii*, and terminates in the antecubital fossa by dividing into the *A. radialis* and *A. ulnaris*.

Curving laterally beneath the short head of the biceps, and becoming then for the first time clearly separated from it, the coracobrachialis is found to insert on the anterior and medial aspect of the humerus between the origins of the brachialis and the medial head of the triceps. The coracobrachialis is supplied by the *N. musculocutaneus* which curves around it laterally or pierces the insertion, giving off muscular branches to both heads of the biceps at this level and continuing medially and distally

to the middle third of the arm where it is joined by a branch of the median nerve. This combined trunk supplies the lower part of the *M. brachialis* and continues to the lateral side of the long head of the biceps where it pierces the deep fascia of the lower third of the arm to supply the skin in this region and in the antecubital fossa. The median nerve likewise gives off a stout branch in the middle third of the arm which passes laterally beneath the biceps to reach the antecubital fossa. This branch continues down the volar surface of the forearm to the wrist as the anterior antibrachial nerve—it usually branches into two parallel rami in the forearm.

On reflecting the brachial artery and vein and the median nerve laterally the entire course of the ulnar nerve to the elbow is exposed. This lies first medial to the vein, then behind it, lying beside the radial nerve to the point where the latter passes posteriorly with the *A. profunda brachii*. From that point it lies on the anterior border of the medial head of the triceps, parallel to the tendon of the dorso-epitrochlearis and passes posteriorly behind the medial epicondyle. The ulnar nerve gives off no branches in the arm.

#### *Lateral and Dorsal Aspect of the Arm.*

The muscles presenting on the dorsal and lateral aspect of the arm are the brachialis and triceps. The origin of the former encircles the insertion of the deltoid superiorly and occupies the lateral and anterior aspect of the humerus deep to the biceps. From the curving lower margin of the spinal portion of the deltoid the long and the upper part of the lateral heads emerge and soon fuse. From between the lateral head of the triceps and the brachialis the lateral cutaneous branches of the radial nerve emerge to supply the skin in this region. From between the lateral head of the triceps and the brachialis below, in the supracondylar region additional lateral brachial cutaneous rami appear. Still lower the lateral and dorsal antibrachial cutaneous nerves spread out fanwise over the lateral and dorsal aspect of the upper third of the forearm. The cephalic vein passes superiorly over the brachialis to attain the groove between the deltoid and pectoralis major.

The *M. triceps* may now be described in its entirety. The spinous and infraglenoid origin of the long head have been noted before; the long head fuses with the lateral head on a level with the lowest point of insertion of the deltoid. The lateral head arises from a point inferior to the greater tuberosity of the humerus and on a level with the attachment of the capsule of the shoulder joint. This origin is essentially on the posterior surface of the humerus, by a narrow strip of aponeurotic tendon that

is fused with the tendon of insertion of the deltoid. Distally, the origin moves laterally and occupies the middle third of the lateral border of the humerus. It shares the lateral intermuscular septum here with the *M. brachialis*. The medial head in *Lagothrix* is essentially a separate muscle. Its origin begins on the same level as that of the lateral head, but medial to it as far as the medial lip of the bicipital groove. From this point distally it occupies an extensive area on the postero-medial aspect of the humerus almost to the olecranon fossa. It forms a stout tendon which encircles the olecranon and inserts separately and deep to the tendon of the long and lateral heads. The lower portion of this medial tendon is split by a branch of the *A. ulnaris collateralis* (three specimens). Some of the lower muscle bundles arising from the medial supracondylar ridge insert still more deeply on the capsule of the joint posteriorly.

The *Mm. anconeus lateralis* and *medialis* are essentially alike in representing further muscle bundles of the triceps complex. Each arises from the corresponding epicondyle and from the capsule of the elbow joint. They insert on the lateral and medial borders of the ulna respectively. These muscles form the superficial covering of the tunnel through which the *Aa. recurrens ulnaris* and *radialis* pass to join the anastomotic rete about the elbow joint.

The triceps complex is supplied by the *N. radialis* and the *A. profunda brachii*. The two bear important relationships to the triceps. At the junction of the upper and middle thirds of the arm, the artery and nerve pass posteriorly between the long and medial heads of the triceps. The radial nerve has already given off rami to the *M. dorsopitrochlearis* and to the long and lateral heads. In the intermuscular canal the *A. profunda brachii* gives muscular branches to the triceps and to the dorso-epitrochlearis; somewhat lower, the *A. collateralis radialis* arises. This latter emerges from the lower border of the lateral head of the triceps and passes distally to join the anastomotic rete about the elbow joint.

In the middle third of the arm the radial nerve and profunda brachii lie in the radial groove of the humerus in direct contact with the bone and covered here by the conjoint bellies of the long and lateral heads of the triceps. In the lower third of the arm, the *N. radialis* approaches the surface in the angle formed by the divergence of the lateral head of the triceps and the *M. brachialis*. For a distance of a centimeter or so the *N. radialis* is exposed in this lateral area, lying parallel to the border of the brachialis. It then plunges deeply once more beneath the origin of the *M. brachioradialis* to enter the forearm. The lateral antibrachial cuta-

neous and dorsal antibrachial cutaneous nerves are given off in this area.

The insertion of the *M. dorsoepitrochlearis* is on the medial aspect of the base of the olecranon process. In addition to extending the forearm, it is clear that this muscle will assist the biceps in supinating the forearm.

#### *The Forearm.*

On removing the integument, the forearm is seen to be sheathed in a stout fascial sheath having strong attachments to the bony prominences of the humeral epicondyles, the olecranon and the borders of the subcutaneous surface of the ulna. There are strong thickenings forming dorsal and volar transverse carpal ligaments.

Just distal to the antecubital fossa, on the medial aspect of the forearm, the prominent *lacertus fibrosus* of the biceps muscle can be traced across the flexor group of muscles almost to the medial border of the ulna, where it fuses with the deep fascia. A short distance proximal to it the medial antibrachial cutaneous nerves pierce the deep fascia and are distributed to the skin over the dorsum of the forearm distal to the olecranon, and to the medial aspect of the forearm for the proximal two-thirds of its length.

Attempts to remove the fascial sheath of the muscles of the forearm reveal the importance of this coat as an origin for some of these and the comparative rigidity of the compartments in which the individual muscles are contained. This is especially true of the flexor group which can be separated only with difficulty from each other since neighboring ones take origin from common intermuscular septa.

When the deep fascia is removed the muscles of the forearm are seen to be divisible into three general groups. First, those which originate on the medial epicondyle of the humerus consisting of the flexors, and held in place by the fascial sheath which is firmly attached to the medial aspect of the subcutaneous surface of the ulna. The second consists of the extensor group of muscles which arise from the lateral epicondyle. Their fascial sheath has its strongest attachment to the lateral aspect of the subcutaneous border of the ulna. The third group consists of a single muscle, the brachioradialis, which has a broad, fleshy origin from the humerus on the upper part of the lateral epicondylar ridge and in part medially from the tendon of insertion of the *M. brachialis*. In the tunnel between these two heads of origin the radial nerve passes into the forearm to join the radial artery and vein.

If the biceps is reflected laterally, the median nerve, and the brachial artery and vein medial to it, are exposed lying on the

brachialis tendon. Just proximal to the bifurcation the brachial artery gives off the *A. collateralis ulnaris*. This is a slender branch passing over the medial head of the triceps. It joins the ulnar nerve and passes behind the medial epicondyle to anastomose with the *A. recurrens ulnaris*. Immediately after its origin the *A. radialis* passes laterally across the median nerve and the tendon of the *M. biceps*, joining the radial nerve behind the *M. brachioradialis*. At this point it gives off the *A. recurrens radialis* which turns back at once and passes lateral to the tendon of the biceps and of the brachialis to join the anastomosis about the elbow. The *A. radialis* also gives muscular branches here to the *M. supinator* and to the brachioradialis before continuing distally in the forearm.

In the region of the bifurcation of the brachial artery in the arm, the *A. ulnaris* gives off the *A. collateralis ulnaris inferior* which passes medially under the tendon of the medial head of the triceps, giving off, as it passes, a slender branch to the adjacent origins of the *M. pronator teres*. If the *M. brachialis* is rotated laterally just above the point of formation of its tendon, a bare area of the humerus may be observed; there are no muscular attachments in this region. Here also the median nerve gives off muscular branches to the *M. pronator teres* before passing deeply in the angle formed by the insertion of this muscle on the radius. The tendon of insertion of the *M. brachialis* is partially revealed passing obliquely downward in the antecubital fossa. It is seen to consist of very stout fibers forming a thin knife-like edge with the sharp edge presenting distally and following its oblique course posteriorly to insert on the coronoid process of the ulna. The similarly flattened tendon of the biceps lies in the same sagittal plane, passing to its insertion on the *tuberositas radii*.

The *M. pronator teres* forms the medial boundary of the antecubital fossa. It arises by stout fleshy fibers from the medial epicondyle of the humerus. Its fibers sweep laterally and the upper ones insert on the deep or medial surface of the radius while the lower ones, which arise in part from the medial epicondyle and in part from the intermuscular septum between this muscle and the origin of the *M. flexor carpi radialis*, form a broad, flat aponeurotic tendon which inserts on the lateral border of the curve of the middle third of the radius. On reflecting the origin from the medial epicondyle a stout tendon is revealed lying on the deep surface of the muscle. Extending from a medial position this tendon passes through the mid portion of the muscle to insert on the radius and form a bridge beneath which the ulnar artery and median nerve pass. It should be noted that the lower third of the



medial border of this muscle presents a thin, free margin.

When the pronator teres is reflected, the first part of the ulnar artery and median nerve are revealed. The artery soon joins the nerve and the two proceed distally together in the forearm, deep to the flexor group and parallel to the ulna. In this region there are muscular branches of the median nerve to the flexor muscles.

The *M. flexor carpi radialis* originates from the medial epicondyle and from the intermuscular septa which separate it from the pronator teres laterally and the flexor digitorum sublimis medially. It is a thin rounded muscle which becomes flattened near the wrist and passes laterally to insert on structures of the wrist region to be described with that part. It is innervated by the median nerve.

The *M. flexor digitorum sublimis* occupies the next medial compartment of the flexor group. It has a narrow fleshy origin from the medial epicondyle and a broad flat aponeurotic tendon of origin from the ulna. This latter extends from a region about a centimeter from the olecranon to within an equal distance from the radio-ulnar joint. It is richly supplied by the median nerve and the ulnar artery gives off its muscular branch near the middle of the belly. In the oval hiatus created by the humeral and ulnar origins of this muscle, the muscular branches of the ulnar nerve to the flexor carpi ulnaris pass to that muscle.

When the flexor digitorum sublimis is reflected the humeral origin of the flexor digitorum profundus is observed to be a fleshy bundle which shares a common tendon with the humeral head of the sublimis. The humeral head of the flexor digitorum profundus becomes flattened distally and terminates in a flat tendon which emerges with the principal tendon of its deeper origins.

#### *Relation of Nerves and Arteries to These Structures.*

The median nerve lies deep to the humeral head of the flexor digitorum sublimis for most of its length in the forearm, passing laterally in the lower third to occupy a median position beneath the tendon of the flexor carpi radialis. In this region it gives off superficial cutaneous branches to the volar surface of the wrist and proximal part of the palm of the hand.

There are fine branches of the median nerve which pass in recurrent fashion about the ulnar artery at the point where it gives off muscular branches to the flexor digitorum profundus. These run backward proximally to the elbow joint in the region where the ulnar nerve enters the forearm. At the point where these recurrent articular branches turn proximally, the ulnar artery gives off the *A. interossea communis*.

This may arise as a single trunk dividing at once into the *Aa. interossea volaris* and *dorsalis*, or these may arise separately from the ulnar artery. Beyond this point the ulnar artery proceeds medially to join the ulnar nerve passing beneath the humeral head of the flexor digitorum profundus. From this point on the artery courses distally to the wrist with the nerve, deep to the ulnar origin of the flexor digitorum sublimis and gives off prominent muscular branches to this muscle at the point of junction with the ulnar nerve.

The *M. flexor carpi ulnaris* is the last superficial muscle of the flexor group. This takes origin from the most posterior part of the medial epicondyle of the humerus and from the major part of the medial border of the subcutaneous surface of the ulna. Its tendon of insertion passes volarward to insert on structures of the wrist which will be described with that region.

The *M. palmaris longus* is a thin and variable muscle, sometimes absent or fused with the flexor carpi ulnaris. It arises from the medial epicondyle and lies superficial to the other flexors. It soon gives rise to a thin, flat tendon that passes over the transverse carpal ligament to insert on the palmar aponeurosis. These two muscles are supplied by the *N. medianus*.

#### *The Extensor Group.*

Arising from the lateral supracondylar ridge of the humerus, just below the origin of the brachioradialis, is the thin and narrow *M. extensor carpi radialis longus*. In the middle of the forearm this muscle gives rise to a narrow tendon which pursues a distal course parallel to the next muscle.

The *M. extensor carpi radialis brevis* takes origin by a few fibers from the supracondylar ridge, but in the main from the lateral epicondyle and in part from the intermuscular septum which it shares with the next muscle. While the brevis is a stouter muscle than the longus, its tendon likewise begins in the middle of the forearm. However, bipenniform fibers continue to join this tendon almost to the wrist. It accompanies the longus into the wrist. Both of these muscles are innervated by the radial nerve and supplied by the radial artery.

The *M. extensor digitorum communis* arises by a stout, flat aponeurosis from the lateral epicondyle just posterior to the preceding muscle. It is a narrow muscle sharing the intermuscular septum with the extensor carpi radialis brevis and continues as one muscle almost to the wrist. Just above the dorsal carpal ligament, however, two bellies diverge and give rise to closely compressed bundles of tendons which enter separate compartments of the ligament. The nerve supply is furnished by the *N. radialis*.

The *M. extensor carpi ulnaris* arises from

the posterior aspect of the lateral humeral epicondyle and for a short distance its proximal portion takes origin from the sheet of the deep fascia that binds it to the lateral border of the ulna. This thin narrow muscle runs parallel to the others and the flat tendon passes somewhat medially over the head of the ulna to the medial side of the wrist.

When the origins of the last two muscles are separated, the dorsal interosseus artery is revealed emerging from between the *M. supinator* and the ulnar head of the abductor carpi radialis. This gives muscular branches to the *M. extensor digitorum longus* and the *M. extensor carpi radialis*. Both of the latter muscles are innervated by branches of the *N. radialis* which pierce the ulnar head of the *M. supinator* to reach the dorsum of the forearm. These branches are from the ramus profundus of the radial nerve.

Reflection of the origins of the extensor muscles reveals the extensive origin of the *M. supinator*. This arises by a wide, fleshy and aponeurotic origin from the lateral epicondyle of the humerus and surrounds the radio-humeral articulation on all but its dorsal aspect. It arises in part, also, by a deep head from the upper third of the ulna. The more medial fibers arising from the epicondyle pass in a sagittal direction distally to insert on the medial aspect of the radius. It is likely that these fibers act to flex the forearm. On the mediolateral aspect of the muscle there is a stout tendinous band which passes almost uninterruptedly to the radial insertion. It is beneath this that the ramus profundus of the radial nerve passes to the dorsum. The *M. supinator* is innervated by the radial nerve and supplied by the radial artery.

The deep muscles of the dorsum of the forearm are the abductor carpi radialis and a muscle complex to be described presently. The former arises by a long narrow head from the lateral aspect of the ulna, from a point on a level with the head of the radius for the full extent of the upper third of the ulna. From this point on it verges laterally, taking origin in part from the interosseus membrane and in the middle third of the ulna by an aponeurotic sheet. Fleshy fibers again take origin from the lower third of the ulna almost to its head. The radial head begins narrowly along the border of the insertion of the *M. supinator* and continues distally over the middle third of the radius. Beyond the *M. supinator*, this margin of the muscle is free. The two heads converge on a central tendon which moves laterally to occupy the lateral border of the muscle where it crosses over the *Mm. extensores carpi radialis longus* and *brevis* to enter a compartment of the dorsal ligament of the wrist. Beyond this the tendon passes in its own serous sheath divided into two

which insert on the *Ossa multangulum majus* and *minus*. The tendon is crossed in this region by the radial nerve and artery.

The last deep muscle is a complex extensor which arises from the middle third of the ulna along its lateral border lying deep to the extensor carpi ulnaris. Near the wrist this gives rise to two tendons; the lateral passes in a separate compartment in an oblique direction laterally beneath the compartment containing the *M. extensor digitorum communis*. The medial tendon and the tendon bundle of the latter muscle pass through the same compartment. These are the *Mm. extensor indicis proprius* and *extensor pollicis*. Both of these deep muscles are innervated by the ramus profundus of the *N. radialis* and supplied by the *A. interossea dorsalis*.

#### *Extensor Tendons on the Dorsum of the wrist.*

The relation of the tendons of the extensor muscles in their respective synovial sheaths as they pass through the dorsal (radio-ulnar) ligament are as follows from the lateral to the medial side:

The tendon of the abductor carpi radialis divides into two distinct tendons proximal to the point of entrance into the carpal sheath. The more lateral of these inserts proximal to the medial one. Its fibers originate entirely from the radius, and while there are mutual insertions of the fibers of the radial and ulnar heads on the tendons of the other, these may be considered as two separate muscles. The tendons enter the common sheath obliquely and course in a groove on the dorsum of the ulnar head. Both insert on carpal bones, the medial and longer tendon curving over to the volar surface of the wrist where it inserts on the *Os multangulum minus*. The proximal tendon inserts on the *Os multangulum majus*.

The *M. abductor carpi radialis* corresponds to the *Mm. abductor pollicis brevis* and *longus* in man. I have chosen to call it the carpal abductor, since it has its principal insertions on the carpus and it is evident that its most important action is to abduct the hand rather than the pollex or the first metacarpal alone. Even though there may be fibers of insertion on the base of the first metacarpal, the strength of the carpal unit insures the movement of the entire mass rather than that of the comparatively weak pollex. It also extends the wrist when the latter is fixed by the extensors and the *M. extensor carpi ulnaris*.

Beneath the tendons of the abductor carpi radialis, the tendons of the extensor carpi radialis longus and brevis pass in their own sheath. As they emerge on the dorsum of the hand they separate from one another, the longus inserting on the carpo-metacarpal joint and on the base of the second meta-



carpal bone. The brevis inserts correspondingly on the third metacarpal bone and the carpo-metacarpal joint.

Crossing over the insertion of the *M. extensor carpi radialis brevis*, two tendons are observed to diverge near the middle of the second metacarpal bone; the lateral one is the tendon of the *M. extensor pollicis*, the medial one is the tendon of the *M. extensor indicis proprius*. Just before the latter passes to the index it sends an extension into the medial aspect of the tendon of the extensor pollicis. On tracing these tendons backward to the proper carpal canal, they are found to arise from the single deep muscle in the forearm arising from the middle third of the ulna. This lies parallel to the extensor muscle that with it occupies the deepest compartment of the dorsal canal. This latter muscle joins the tendon of the extensor digitorum communis.

The tendons of the extensor digitorum communis occupy the central compartment and these are joined on the deep surface by the tendon passing to the index and pollex. This latter divides into three, the lateral joining the under surface of the tendon to the index, the other two proceeding to the third and fourth fingers respectively. The tendon of the extensor digitorum communis itself divides immediately into five divisions which are distributed as follows:

The first passes to the index alone after giving off the connecting band to the tendon of the third finger. The second division passes exclusively to the middle finger. The third straddles the third and fourth, giving tendons to each. The fourth gives a contribution to the fifth in the metacarpal region and then passes directly to the fourth finger. The fifth straddles the fourth and fifth digits, giving tendons to each.

The medial part of the extensor digitorum communis may be considered as a separate muscle although it has a common origin with the communis. However, its belly may be separated almost the entire length of the forearm and it passes through a separate, more medially placed compartment in the wrist. In the carpal region the tendon divides to give a lateral tendon to the fourth finger which passes deep to the tendon of the extensor digitorum communis and a medial one which may be considered as constituting the tendon of the *M. extensor digiti quinti*.

The most medial compartment of the dorsum of the wrist is occupied by the tendon of the extensor carpi ulnaris. This courses medially in an oblique direction in its groove on the head of the ulna to pass volarward and inserts on the volar surface of the base of the fifth metacarpal.

Each common extensor tendon spreads out in a flat sheet over the metacarpophalan-

geal joint. This sheet is continued over the proximal phalanx and extends volarward with well defined margins on each side about half the thickness of the digit. This sheet inserts laterally on the base of the second phalanx. The central dorsal portion continues as a long triangular extension passing over the dorsum of the second phalanx; its base inserts on the base of the distal phalanx.

#### *The Dorsal Carpal Ligament.*

The dorsal (transverse) carpal ligament is exceptionally stout and provides firm restraint for the extensor tendons. There are three major and distinctly separate parts. The first extends from a ridge on the medial side of the base of the radius over the extensor tendons, the head of the ulna, and inserts on the apex of the *Os triquetrum* below the *Os pisiforme*. The second arises from a point distal to the origin of the first, beneath the tendon of the extensor carpi radialis brevis. This ligament extends medially parallel to the first; its insertion is broader than its origin. The proximal attachment is to the head of the ulna and distally it curves about the extensor tendons to form the medial wall of their restraining canal, inserting on the carpus. The third originates on the base of the radius lateral to the tendon of the extensor carpi radialis longus and inserts in part on the lip of the groove in which the tendon of the abductor carpi radialis is confined and continues distally to insert on the *Os multangulum majus*. A fourth component covers the groove in which the tendons of the *Mm. extensor carpi radialis longus* and *brevis* lie.

The divisions of the extensor tendons of the hand have important functional implications. The existence of a separate, common extensor of the pollex and index helps to explain the observation that these two digits act as a joint unit. Further, its ulnar origin and the lateral course of its tendons serve to abduct this thumb unit of the hand from the remainder of the digits. The common extensor of the digits arises from a region that is medial with respect to the origin of this muscle and yet the tendons of both are fixed in the carpal canals at essentially the same point. Thus, when the muscles contract they are exerting their effective pull in essentially opposite directions.

The only hint of functional independence of the remaining digits is that when separated by rough dissection, the muscular bellies of the individual parts are found to originate from progressively dorsal positions on the lateral epicondyle, those of the fourth and fifth fingers become fleshy at a point considerably below the bellies of the bundles going to the second and third fingers. The common origins from intermuscular septa and the firm sheath in which

they are held makes the functional interpretation of these details difficult.

The *Mm. extensor carpi radialis longus* and *brevis* not only extend the hand, but when the latter is in a position of radial deviation, they tend to adduct it in an ulnar direction and bring it into the median axis. The same is true when the hand is in the position of ulnar deviation.

When the principal extensors of the digits are elevated from their canal in the wrist, it is clear that the depth of this passage with the firm bony walls formed by the grooves in the base of the radius and the head of the ulna and the strong ligamentous roof provide fulcra which direct the effective pull of the muscles. Examination of the origins and insertions of the respective muscles makes clear the combined extending and separating action. The extensor digiti quinti takes origin lateral to the median axis of the wrist, but its insertion is well to the medial side of the axis; its tendon passing through the canal is firmly held in the median line and hence abduction of the fifth occurs with extension, when the exclusive motion of this digit effected by the extensor is considered. The origin and insertion of the extensor pollicis and indicis are the direct opposite of the foregoing, but the essential movement is of the same nature, combined extension and abduction.

The interlacing fibers between the tendons to the third and fourth fingers indicate in my opinion a relative interdependence between the motion of extension of these fingers produced by their extensors. That is, extension of one without simultaneous extension of the others would appear to be impossible anatomically. While the axis of effective pull of the extensor indicis proprius points to an independent motion, in association with that of the pollex, the equally strong tendinous contribution from the extensor digitorum communis suggests a beginning transition to an association of the movements of this finger with that of the others opposed to the thumb. The modification of these considerations by the action of the intrinsic muscles of the hands will be discussed elsewhere.

When the extensors are reflected, a long branch of the ramus profundus of the *N. radialis* is revealed on the deep surface of the *M. extensor pollicis et indicis* and may be traced to the dorsum of the wrist, the hand and into the wrist joint itself. The terminal branch of the *A. interossea volaris* emerges from the lower margin of the *M. abductor carpi* and anastomoses with the superficial branch of the radial artery and other contributors to the *Rete carpi dorsalis*. The superficial branch of the *A. radialis* which curves dorsally over the base of the radius to gain the dorsum of the hand, passes superficial to the tendons of the *M.*

*extensores carpi radialis longus* and *brevis* and turns medially forming the *Arcus carpi dorsalis*. It continues medially deep to all the extensor tendons and anastomoses with the ramus dorsalis of the *A. ulnaris*. On the dorsum it sends anastomotic rami proximally to the *Rete carpi dorsalis* and at each interspace including the first, gives off *Aa. metacarpi dorsales*. Each of these gives off a digital artery to the corresponding side of the digits and perforating branches which pass between the heads of the metacarpals to anastomose with the volar metacarpal arteries.

#### *Superficial Structures of the Palm.*

The skin of the palm is densely attached to the palmar fascia and bound to the first and fifth metacarpal bones and to the volar carpal ligament at the wrist. When this is removed the strong palmar aponeurosis is revealed occupying a central position over the carpus and metacarpal areas. There are extensions of variable strength and prominence reaching the bases of the digits. Arising from the ulnar margin is the *M. palmaris brevis* which passes medially to insert on the skin of the medial border of the palm. It is innervated by the ulnar nerve. The palm is well padded with lobules of fat which are held in firm compartments of fibrous tissue. These pads of fibro-adipose tissue emerge between the four principal extensions of the palmar fascia running to the bases of the second, third, fourth and fifth digits. The pads receive a rich nerve supply from the metacarpal divisions of the nerves of the palm.

When the palmar fascia is severed in the middle of the palm and reflected distally it is seen to be tightly bound to the medial side of the palm by stout projections that insert on the lateral border of the fifth metacarpal and by deep extensions it is firmly bound to the metacarpo-phalangeal joints. Proximally the palmar fascia is fused with the transverse carpal ligament which forms the volar roof of the carpal flexor canal.

Medially, the ulnar artery emerges to give rise to the *Arcus volaris superficialis*. This curves laterally over the palm and is visible between the digitations of the palmar aponeurosis. It gives off *Aa. metacarpi volares*, each of which terminates in the corresponding interspace to give rise to the *Aa. digitales volares propriae*. Emerging with the ulnar artery is the *N. ulnaris* which gives off terminal branches to the lateral side of the fifth digit, the medial side of the fourth digit and after joining with a stout branch of the *N. medianus*, supplies the lateral side of the fourth digit and the medial side of the third digit. It should be noted that the *N. ulnaris* passes in a superficial compartment over the transverse carpal ligament, while the *N. media-*

*nus* passes through deep to this ligament in company with the flexor tendons. The median nerve supplies in the hand, the lateral side of the thumb by an independent branch, the medial side of the thumb and the lateral side of the index, the medial side of the index and the lateral side of the middle finger and, in conjunction with the ulnar, the medial side of the middle and lateral side of the ring finger. The superficial branch of the *N. ulnaris* passes beneath the ulnar artery and the *Arcus palmaris superficialis* to the lateral side of the fifth finger and medial side of the fourth.

On reflection of the palmar fascia in the proximal part of the palm, the relations of the *N. medianus*, *N. ulnaris* and the *A. ulnaris* are revealed. The superficial branch of the median nerve passes medially over the tendon of the *M. flexor digitorum sublimis* under which it has coursed up to this point. It is joined, beneath the insertion of the *M. flexor carpi ulnaris* on the *Os pisiforme* by the ramus palmaris of the ulnar nerve and the ulnar artery. These enter a compartment beneath the overhanging *Os pisiforme*. Here there are plexiform branches of the median nerve that pass to the ulnar nerve. The ulnar nerve divides to give off a superficial branch which passes to the medial side of the fifth finger and a deep branch which passes dorsally between the *M. abductor digiti quinti* and the *M. flexor digiti quinti brevis*.

The floor is formed by the stout transverse carpal ligament. This has exceedingly strong attachments to the carpus and forms the roof of the deep carpal canal through which the tendons of the flexor muscles pass.

If the transverse carpal ligament is divided longitudinally, the carpal canal and its contents are revealed. The canal is smoothly lined and its thickness and rigidity clearly act as a restraint to the flexor tendons. Lying on the tendons superficially the *N. medianus* is loosely bound to them by loose areolar tissue. This emerges in the palm below the distal border of the transverse carpal ligament and divides to form three metacarpal branches passing to the first, second and third interspaces and corresponding sides of the thumb and fingers. A fourth branch gives off the muscular supply to the *M. flexor pollicis brevis* and continues distally to supply the lateral aspect of the thumb. The most medial branch is joined by a branch of the superficial ramus of the *N. medianus*. It is probable that these plexiform intercommunications have no great functional significance aside from the obvious overlapping representation of important sensory areas.

The *M. flexor digitorum sublimis* tendons in the wrist lie superficial to those of the *M. flexor digitorum profundus*, but in the

carpal canal they lie medial to the latter. The flexor sublimis may be reviewed now that it is revealed in its entire length. The four tendons to which it gives rise may be followed proximally into four distinct bellies, but of these latter only that whose tendon passes to the index remains comparatively distinct in its entirety. In the canal the tendon to the index lies deep to the other three and arises from that part of the muscle lying most deeply and constituting the part taking origin from the ulna. However, the pointed upper extremity of the belly joins with the others to take origin from the medial epicondyle of the humerus. The strong flat tendon forms on the lateral aspect of the muscle, the lower fibers of which take origin directly from the ulna. It would seem that these tend to draw the index toward the midline or median axis of the hand when flexing the digit.

The remaining tendons and the bellies from which they derive are as follows: The division for the fifth digit is the most medial and superficial. It takes origin from the strong aponeurotic covering of the muscle which fixes it to the epicondyle. This aponeurosis sweeps medially to attach to the ulna and the lower fibers of this belly arise from it. The intermediate belly takes origin solely from the humeral epicondyle and in its upper part lies superficial to the division going to the middle finger. The latter is a typical bipennate muscle deriving its fibers of origin chiefly from the epicondyle, deep to the last muscle, but in addition receives a sheaf of fibers from the common aponeurotic tendon of this muscle attaching to the ulna. Its fibers pass deep to those of the index division. The tendon comes to lie lateral to those to the fourth and fifth finger. These tendons as they lie in the carpal canal are simply held together by loose areolar tissue. There is apparently no synovial sheath.

When the flexor sublimis is elevated the common tendon of the *M. flexor digitorum profundus* is found to lie in part lateral and in part deep to that of the sublimis. The two separate and distinct bellies of this muscle as seen in the forearm, the one arising from the entire length of the radius and by a deeply lying humeral head, the other arising from the entire length of the ulna, are easily separable from one another. The rami of the *N. medianus* enter the bellies at a point above their juncture in the upper third of the forearm. In the carpal canal, however, the tendons of these two join by a broad union to form a single flat band which immediately divides into five individual tendons. When the tendons are severed in the wrist and displaced distally, the deep surface presents an interesting complexity.

Medially the tendon of the *digiti quinti*

may be traced directly from the lateral portion of the ulnar division of the muscle, and this may be traced as a separate muscle belly in the forearm lying medial to the others. However, this tendon sends a prominent contribution to the tendon of the fourth finger. The latter is formed of the remaining bundles from the ulnar division and from a stout contribution of the radial muscle. The tendon of the middle finger proceeds directly from the radial muscle, and the fibers of this tendon and that of the index are in part seen to curve posteriorly from the anterior part of the muscle. Thus, the tendon of the pollex is partially sheathed in its first portion. It should be pointed out here that there is no tendon of the flexor digitorum sublimis to the thumb.

This interlacing structure of the tendons no doubt serves to reinforce the combined grip of the individual fingers. The flexor profundus may be thought of as a muscle chiefly employed for climbing and hanging suspended, actions which involve all the fingers at once and require none of the refinements of independent motility.

The tendons in the carpal canal are not surrounded by a sheath, and the *Vaginae propriae* of the deep tendons do not begin until the point at which they are joined by the tendons of the *M. flexor sublimis*; both tendons enter a common sheath at this point. The fibers passing to the tendon of the index curve from the antero-lateral aspect of the common tendon, around the tendon of the pollex. The lowest muscle fibers arising from the radius curve medially and posteriorly to be continued as the tendon of the index. Thus, the tendon of the thumb arises from that portion of the muscle lying on the anterior surface toward the mid-line. The tendon of the third finger is derived from that portion of the muscle lying most medially and the fibers may be traced chiefly to the humeral head. The tendon of the fourth finger receives a contribution from the tendon of the fifth, which joins the remaining fibers of the ulnar muscle, and the stout tendon which passes to it from the radial muscle on the deep surface of the tendon mass.

The four *Mm. lumbricales* consist of thin spindle-shaped muscles taking origin from the bifurcation of the tendon of the extensor digitorum profundus and for a short distance from the adjacent sides of these. They lie in the space between these tendons until they reach the metacarpo-phalangeal joints where they enter a canal or sheath formed by extensions of the fascial slips from the digitations of the palmar fascia where it becomes firmly attached to the joint capsule.

Between the heads of the metacarpals there are well-defined intercapitular liga-

ments consisting of flat sheets blending with the metacarpo-phalangeal joint capsules. These sheets form slings in which the lumbrical muscles rest, separating them from the deeper intrinsic muscles. The lumbricales pass in separate fibrous compartments over the antero-lateral aspect of the metacarpo-phalangeal joints to insert in each case on the volar border of the extension of the broad tendon of the *M. extensor digitorum communis*. A single exception is the fourth lumbrical which has been found to insert in one case on the lateral aspect of the proximal phalanx of the fifth digit rather than on the adjacent extensor tendon. With the fingers flexed on the palms the lumbricales serve to extend the second phalanx on which this portion of the extensor tendon inserts. The first lumbrical inserting on the index, by reason of its origin well to the medial side of the axis of this finger, will produce some degree of abduction also.

In the middle of the palm the tendons of the flexor digitorum sublimis join the tendons of the flexor digitorum profundus and at this point the sheath of the latter opens and extends deeply to include the two tendons which from that point to their insertions occupy a common sheath. Over the metacarpo-phalangeal joint the sheath presents a circular thickened band which strongly confines the tendons; beyond this the capsule again becomes thin and membranous. Similar annular ligaments are found at each interphalangeal joint. At points between these there are additional annular ligaments near the middle of the proximal and middle phalanges. These correspond to the ligamenta cruciata in man, but in *Lagothrix* they are simple circinate bands which are firmly attached to the borders of the groove in which the tendons lie. Near the middle of the proximal phalanx the overlying tendon of the flexor sublimis divides to permit the tendon of the flexor profundus to emerge and continue its central course to insert on the base of the distal phalanx. It also is divided and the two parts diverge slightly at the point of insertion. The two parts of the flexor sublimis occupy positions on each side of the deep tendon. At the middle of the second phalanx the tendon of the profundus spreads out, partially covering the insertion of the sublimis on the margins of the volar groove of the phalanx in which the tendons lie. The flexor tendons possess well-developed *vincula* passing to their under surfaces from the hollow of the sheath. There is one from the middle of the proximal phalanx to the sublimis tendon at the point of division and a second just proximal to the first interphalangeal joint. A third joins the tendon of the profundus proximal to the second interphalangeal joint.

The tendon of the pollex deriving from radial division of the flexor digitorum profundus passes unaccompanied to the thumb. There are the usual annular ligaments over the joints and a single very stout annular ligament binding the tendon firmly to the distal half of the proximal phalanx. Here, too, the tendon shows the usual division of the deep tendons and inserts similarly on the distal phalanx, but at a point somewhat nearer the distal tip.

Removal of the flexor tendons reveals the first layer of the intrinsic muscles of the hand forming the floor of the palm. The most prominent of these is the fan-shaped *M. adductor pollicis*. This muscle is variable in extent, but occupies roughly half of this region of the palm. It is triangular in shape and consists of four heads of inconsistent shape, although the origins and general configuration are readily identified in each case thus far examined. The proximal head takes origin from the carpo-metacarpal ligament at the base of the third metacarpal and courses distally on the upper portion of the common tendon of the muscle. This head also takes origin from a curved tendon whose concavity is directed medially, extending from the carpo-metacarpal ligament to terminate in the joint capsule of the fifth metacarpophalangeal joint. The second head takes origin from the convex border of the curved tendon. The third and fourth arise variably from this tendon or from separate tendons, the third from the base of the fifth finger and fourth from the region of the fourth metacarpophalangeal joint. The fibers of each converge on the common tendon which is inserted on the medial aspect of the base of the proximal phalanx of the thumb and in part upon the extensor tendon. It is innervated by the ramus profundus of the ulnar nerve as this crosses the palm; the nerve enters the deep surface of the muscle.

When the *M. adductor pollicis* is reflected, a bicapitate muscle is revealed arising from the upper portion of the curved central tendon from which the *M. adductor pollicis* also originates and from the slip that takes origin from the base of the fourth finger, converges on a common tendon which inserts on the medial border of the extensor tendon of the index. This is the *M. adductor indicis proprius*. In some cases it inserts largely on the lateral aspect of the proximal phalanx. In some specimens this muscle is as well developed as the adductor pollicis and consists of stout fleshy bellies arising from the entire length of the central tendon from which the adductor pollicis takes origin. In such cases it continues down as a prominent muscle bundle to insert on the medial aspect of the proximal phalanx. This duplication of adductor muscles is strong evidence in

support of the combined action of the thumb and index as a "pollicial unit."

The *M. abductor indicis* takes origin from almost the entire length of the first and second metacarpals and at its proximal tip from the carpus. The fibers converge on a narrow tendon which passes over the lateral aspect of the metacarpo-phalangeal joint. In this region the tendon passes through a fibrous sheath passing over it from the extensor tendon. The abductor indicis is inserted on the strong circular band which surrounds the base of the phalanx and is continued on the volar surface as the annular articular ligament of the flexor tendon. The abductor indicis receives the terminal branch of the ramus profundus *N. ulnaris*. The remaining intrinsic muscles of the palm present a degree of complexity which does not lend itself readily to systematic description. There are three muscular heads taking origin on the same plane as the abductor pollicis and indicis from a central tendon extending from the lower border of the deep transverse carpal ligament. The most medial of these passes to the lateral aspect of the fifth digit where it is joined by a deep head arising from the carpus and from the lateral aspect of the fifth metacarpal. This combined muscle forms a narrow tendon which passes over the lateral aspect of the fifth metacarpophalangeal joint and is inserted on the extensor tendon. It is innervated by the ramus profundus of the *N. ulnaris*. A small slip of the superficial head passes deep to insert on the lateral aspect of the fifth metacarpal just proximal to the metacarpo-phalangeal joint. The second head arising from this common tendon passes to the medial side of the fourth metacarpal where it is joined by a deeper head also arising from the carpus and from the medial aspect of the volar surface of the fourth metacarpal. The tendon formed by these two passes over the antero-medial aspect of the fourth metacarpal joint and inserts on the extensor tendon.

In the fourth interspace the dorsal interosseus muscle, arising from the carpus, the lateral aspect of the fifth metacarpal and the medial aspect of the fourth converges on a stout tendon which passes over the medial aspect of the fourth metacarpo-phalangeal joint and inserts on the base of the proximal phalanx of the third digit.

The third and medial superficial head arising from the central tendon joins a deeper head arising from the carpus and the lateral aspect of the fourth metacarpal. These converge on a common tendon which inserts on the extensor tendon proximal to the insertion of the third lumbrical.

On the medial and lateral aspects of the middle finger there are symmetrical muscles consisting of superficial heads arising from



the carpus and the medial and lateral aspects of the third metacarpal and deep heads which are the dorsal interossei arising from the lateral and medial aspect of the third and fourth and from the second and third metacarpals, respectively. The heads converge on tendons which pass on the corresponding sides of the metacarpo-phalangeal joint to insert on the extensor tendons.

The second metacarpal presents on its medial volar aspect a superficial head corresponding to those described above, originating from the carpus and the medial aspect of the bone and giving rise to a tendon which inserts on the extensor tendon. On the lateral aspect of the second metacarpal there is a similar superficial head with its origin on the carpus and the lateral side of the volar aspect of the bone. This inserts on the volar surface of the proximal phalanx anterior to the insertion of the abductor indicis.

All of these muscles are innervated by the *ramus profundus* of the *N. ulnaris*. This nerve curves laterally beneath the combined aponeurotic tendon of the three superficial heads of the medial group and to the volar surface of the heads of the second, third and fourth metacarpals it gives off a fine branch which terminates in a fibro-fatty pad here or is distributed to the joint. It is impossible to trace these to their termination exactly but it is assumed that they subserve proprioceptive perception.

#### *Intrinsic Muscles of the Fifth Digit.*

The *M. abductor digiti quinti* consists of a fleshy belly constituting the principal muscle mass of the hypothenar eminence. It takes origin from the volar transverse carpal ligament and from the pisiform bone. The slender rounded tendon begins halfway in its length and inserts on the base of the proximal phalanx of the fifth digit. Its functional activity is improved by the passage of this tendon through a firm fibrous ligament which is a continuation of the annular articular ligament of the flexor tendons and by a fibrous sheet extending dorsally from the border of the insertion of the *flexor digiti quinti brevis* into the extensor tendon. It is innervated by the *ramus profundus* of the *N. ulnaris*.

The *M. flexor digiti quinti brevis* arises by an aponeurotic tendon from the transverse carpal ligament. Its origin provides the lateral boundary of the tunnel through which the *ramus profundus* of the ulnar nerve passes. This muscle pursues a somewhat oblique course from its laterally placed origin to its insertion on the medio.lateral aspect of the base of the first phalanx of the fifth digit and on the extensor tendon. It is innervated by the *ramus profundus* of the *N. ulnaris*.

The *M. opponens digiti quinti* lies deep to

the flexor brevis and takes origin from the carpus over the fifth carpo-metacarpal joint. Its fibers insert on the lower half of the volar surface of the fifth metacarpal. The functional significance of the firm fibrous sheath which encloses the muscle is not clear.

#### *Intrinsic Muscles of the Pollex.*

The *M. abductor pollicis brevis* takes origin from the carpus just proximal to the carpo-metacarpal joint and passes obliquely and laterally to insert on the lateral aspect of the base of the first phalanx. Its tendon is held in place by a stout fibrous sheath extending between the extensor tendon and the insertion of the flexor pollicis brevis. It receives its nerve supply from the *N. medianus*.

The *M. flexor pollicis brevis*, which is innervated by the *N. medianus*, takes origin from the volar transverse carpal ligament and passes obliquely to insert in part on the lateral aspect of the proximal phalanx and in part on the extensor tendon. Its insertion partially encircles the tendon of the abductor pollicis brevis.

The *M. opponens pollicis* is a variable muscle, not so well defined as the opponens digiti quinti. It takes origin from the volar transverse carpal ligament deep to the flexor brevis and inserts in some cases on the volar surface of the first metacarpal and sometimes in common with the flexor, but slightly proximal to it on the head of the metacarpal over the joint. Innervation is from the *N. medianus*.

The *Arcus volaris profundus* is formed from a terminal branch of the ulnar artery which accompanies the *ramus profundus* of the *N. ulnaris* beneath the superficial layer of muscles and courses beneath their origins from the medial to the lateral side of the palm supplying fine branches to the intrinsic muscles and numerous contributions to the *rete volaris carpi*. There are also fine metacarpal branches passing to the interspaces where they anastomose with both dorsal and volar metacarpal branches from the superficial volar arch and the dorsal arch.

The *M. pronator quadratus* may be revealed by separating the flexor bellies and reflecting them to either side. It is a quadrilateral sheet of muscle fibers with its origin on the volar surface of the ulna at a point somewhat higher than its insertion on the radius. Thus, the fibers sweep distally and laterally to the volar surface of the distal extremity of the radius across the interosseus membrane. When the muscle is lifted up it is found to arise also from this structure. The insertion on the radius is over a broad area of the volar surface from the lateral to the medial margin. This extensive insertion would seem to signify the importance of this muscle in the initiation as

well as the completion of pronation. It is supplied by the volar interosseous artery and the volar interosseous branch of the *N. medianus*. These latter enter its deep surface and the artery itself terminates in fine anastomotic branches which pass in the medial dorsal compartment beneath the extensor tendons to join the dorsal carpal rete.

#### *The Shoulder Joint.*

The shoulder joint (*articulatio humeri*) is a diarthrosis of the ball and socket type. As in other primates, including man, it depends on the strong muscles surrounding it and the stout tendons of their attachments for its strength. The capsule of the joint itself is relatively loose and is only thickened at those points where the muscular tendons blend with it. It surrounds the glenoid cavity of the scapula and is attached on an oblique line around the head of the humerus. On the antero-medial aspect there is an opening to give exit to the tendon of the long head of the biceps which is intra-articular up to that point from its origin. This tendon passes over the head of the humerus from its origin on the supraglenoid tubercle of the scapula. The second muscle entering into intimate relations with the joint capsule is the *M. subscapularis*. The tendon of this muscle sweeps anteriorly about the neck of the humerus and its upper fibrous border blends with the capsule of the joint. This tendon forms a thickened ligament presenting a free margin within the joint cavity. There is a notch in the edge of the glenoid cavity into which the subscapular tendon fits. The portion of the subscapular tendon forming this ligament can be traced to the scapula and evidently limits external rotation of the humerus, since the muscle fibers are reduced in number in this part of the muscle.

The *Ligamentum acromio-claviculare* has a strong attachment to the anterior tip of the acromion, beneath the acromio-clavicular joint. It curves superiorly to attach to the under surface of the clavicle just proximal to the acromio-clavicular joint, forming the posterior retaining ligament of this articulation.

The *Ligamentum coraco-claviculare* extends from a point on the inferior surface of the clavicle just a short distance beyond the *L. acromio-claviculare* and curves medially to the base of the coracoid process. There is a strong band of fibers which curves upward from the acromion to the clavicle and down to the coracoid process, uniting the foregoing, and while it appears to be a separate ligament, the separation is undoubtedly artificial and this complex may be considered as a unit.

This combined ligament constitutes an arch through which the tendon of the supraspinatus passes to its insertion into the

greater tuberosity. (The deltoid branch of the dorsal scapular nerve passes under this arch also). Posteriorly the joint is covered by the tendons of the supraspinatus, the infraspinatus, and the teres minor. Deep to the first two there are bursae separating the tendons from the joint capsule.

The *Articulatio acromio-claviculare* is a simple diarthrosis with a stout capsular ligament and an articular cartilaginous disc. The tip of the clavicle articulates with the anterior aspect of the tip of the acromion.

#### *The Articulatio Cubiti and Adjacent Deep Structures.*

It is necessary to remove all the muscles about this joint in order to reveal its structures completely, and as this is done the relation of these to the joint may be reviewed. Anteriorly the broad tendon of the *M. brachialis* is found to cross from the lowest point of origin on the anterior aspect of the humerus some distance above the coronoid fossa to its oblique longitudinal insertion on the antero-medial aspect of the ulna. This insertion is about a centimeter in length and begins at a point just beyond the *processus coronoideus*.

The *Articulatio Cubiti* includes the humero-ulnar, the radio-humeral and the proximal radio-ulnar articulations. The *capsula articularis* is relatively more restrictive than the capsule of the shoulder joint and presents a number of thickenings and accessory ligaments which both strengthen and limit the movements of which the joint is capable. There are irregular thickenings between the antero-lateral aspect of the humerus running obliquely to the coronoid process of the ulna. The anterior aspect of the radio-humeral joint is likewise thickened. The latter is exceptionally stout and consists of exceedingly dense fibrous tissue. It is firmly attached to the ulna at each end of the shallow semi-lunar articular facet.

The *ligamenta collateralia ulnaris* and *radialis* consist of strong fan-shaped flat ligaments extending from the inferior aspects of the medial and lateral condyles respectively to the ulna and annular ligament of the radius.

The strongest and most prominent accessory ligament is the *chorda obliqua*. This stout ligament extends between the anterior aspect of the medial epicondyle and the posterior surface of the radial tuberosity proximal to the insertion of the *M. biceps*. Just beyond its attachment to the epicondyle it sends an oblique and medially directed band which passes over the medial aspect of the base of the coronoid process to the ulna. These two limit the extent of supination. In any position, except with the arm in extreme medial rotation, complete supination of the wrist is prevented by this band.

The *Ligamentum annulare radii* is a stout

thickening of the capsule of the radio-ulnar joint. It surrounds the neck of the radius presenting a strong attachment to the base of the coronoid process passing beneath the chorda obliqua.

When the elbow joint is opened anteriorly a very stout, partly intra-articular ligament is found extending fan-like from a broad base in the coronoid fossa. This converges on a narrow rounded band which fuses at right angles with the *Ligamentum annulare radii*. It also sends a slender band of insertion on the lateral aspect of the processus coronoideus of the ulna. The lateral border of this ligament presents a free margin within the joint, but its medial fibers are fused with the part of the capsule over the medial condyle. This ligament has no counterpart in the human being. It definitely limits extension and by the fibers coming from the anterior aspect of the medial epicondyle limits supination as well.

When the joint is fully opened, a thickened fold of the posterior part of the capsule forms a ligament somewhat like the last described. This has a similar concave free margin within the joint. The fold curves from the lateral epicondyle of the humerus medially and downward over the posterior aspect of the articular surface of the ulna. As it crosses over this to insert in the medial border of the *incisura semilunaris*, the medial border of it likewise becomes free and this narrow band of fibrous tissue covered by synovial membrane lies between the articular surfaces of the trochlea of the humerus and the *incisura semilunaris* of the ulna.

Between the head of the radius and the lateral condyle of the humerus, laterally there is a pad of fibro-fatty tissue covered by the synovial membrane, constituting a fold or plica which seems to complete the *incisura radialis*. These folds are present in all of the joints thus far described wherever the irregularities of the bones leave interstices.

The insertion of the tendon of the *M. biceps brachii* is on the dorsal aspect of the tuberosity of the radius. When this tendon is reflected medially a bursa between the tendon and the bone is disclosed. With the forearm fully supinated it is seen that the plane of this insertion lies anterior to that of the brachialis of the ulna, although the lines of insertion are parallel and in pronation they lie in the same antero-posterior plane.

Lateral to the biceps tendon, covering the entire volar surface of the radio-humeral joint and the neck of the radius, is the *M. supinator*. The medial side of this muscle partially encircles the biceps tendon; a narrow bundle of fibers extends downward to insert at the base of the insertion of the chorda obliqua. The principal insertion of

the supinator is wrapped about the lateral volar and dorsal aspect of the upper third of the radius. It meets the insertion of the pronator teres at an acute angle.

The *Membrana interossea* is a stout fibrous sheet extending between the respective *Cristae interossee* of the radius and ulna. The proximal attachment is at a higher point on the radius, just below the radial tuberosity and this free border extends downward obliquely to the ulna. The fibers present an interlacing structure beyond this point. It serves as an additional surface of origin for the deeper volar and dorsal muscles and also limits supination.

### The Wrist Joint.

The wrist is a relatively loose condyloid joint permitting free motion dorso-ventrally and from side to side. Before describing the joint proper, it is convenient to review the terminations of long tendons inserted about the joint.

The tendon of the *M. flexor carpi radialis* may be examined first. This tendon lies on the volar surface of the wrist, entering its own proper sheath and passing through a compartment in the superficial part of the transverse carpal volar ligament. It is retained in this region laterally by the uncinate process of the *Os multangulum majus*. It may give off a slip here to insert in the central portion of the transverse volar carpal ligament and the palmar fascia. (Note: the palmaris longus may be absent). The remainder of the tendon plunges deeply to terminate about the first, second and third carpo-metacarpal joints. Its insertions here are not constant. In some cases there are slight slips to the base of the first metacarpal, but the principal termination is on the base of the second metacarpal. Functionally, it must be recognized that the rigidity of the second, third, and fourth carpo-metacarpal joints renders this insertion essentially that of a flexor of the carpus and of the central metacarpals with the latter.

The tendon of the *M. flexor carpi ulnaris* inserts on the *Os pisiforme* which rests on the volar surface of the *Os triquetrum*. The tendon is continued downward distally to insert on the base of the fifth metacarpal. Here it lies medial to the *hamulus ossis hamatum* and lies in a groove on the lateral surface of this process. (c.f. *infra*: Ligaments of the *Os pisiforme*).

While these flexor tendons insert on opposite sides of the carpus, the pull of the muscles is not only in the direction of flexion, but also of ulnar deviation of the hand and assists in pronation. The pronated position of the hand is most effective in sustaining flexion of the fingers by aligning the strong ulnar origins with the point of chief pull in the carpal canal.



The transverse carpal ligament may be considered as consisting of superficial and deep parts which are fused on the medial and lateral aspects of the carpus to form the flexor tunnel, or as a circular collar resting on the volar aspect of the carpus and held in place by strong attachments to the triquetrum and pisiform medially, the navicular and multangulum majus laterally, and the capitate centrally. It fuses proximally with the capsule of the radio-carpal joint. There is a stout radio-capitate ligament extending from the volar surface of the base of the radius to the volar surface of the capitate bone. When the wrist joint is opened from the dorsal surface a number of important retaining ligaments are revealed. The first of these is the first portion of the dorsal carpal ligament which extends obliquely from the radius to the dorsum of the triquetrum and its continuation in the triquetro-lunate ligament which together form the canal through which pass the tendons of the extensor digitorum communis. When the radio-carpal joint is opened the adjacent articular surfaces of the navicular and lunate are exposed. The concave articular surface of the radius facing them presents about its rim a fibro-cartilaginous labrum. From the edges of this the articular capsule extends to the carpus. The labrum is continuous with the fibro-cartilaginous disc between the base of the radius and head of the ulna and with an inter-articular ligament consisting of two parts. The dorsal portion extends from the radio-ulnar articulation to the triquetro-lunate articulation. The volar portion of this inter-articular ligament is found to consist of the deeper fibers of the radio-capitate ligament. The *articulatio ulno-carpalis* is between the head of the ulna and the triquetrum and pisiform. The ulnar surface is convex, fitting into the depressions of the articular surfaces of the triquetrum and pisiform. This is the reverse of the radio-carpal joint where the concave surface is presented by the radius. The volar ligament extends from the radio-ulnar fibrocartilage to the pisiform and the volar surface of the triquetrum. Further exposure of the joint reveals the volar radio-carpal ligament. This is a fan-shaped ligament extending from the entire width of the radius on the volar aspect of the margin of the articular surface converging on the volar aspect of the lunate.

On the volar aspect of the pisiform there are three stout ligaments diverging distally as follows: The proximal one extends from the pisiform to the *Os multangulum majus*; the intermediate one extends from the pisiform to the proximal aspect of the base of the hamulus of the *Os hamatum*; and the distal one extends to the volar surface of the base of the fifth metacarpal, just beyond the carpo-metacarpal joint.

When the carpal joints are further exposed from the dorsal surface, the hamate and capitatum are found to fit closely to each other and form a rounded proximal surface which articulates with correspondingly concave articular facets of the proximal row. The sharp distal edge of the *Os centrale* forms the lateral lip of this cup and intervenes between the lateral aspect of the *Os lunatum* and the medial aspect of the *Os multangulum minus* and the *Os multangulum majus* which lies somewhat volarward with respect to the lesser multangulum.

The articulations of the metacarpals and the carpal bones are as follows: The first metacarpal articulates exclusively with the *Os multangulum majus*. The second articulates with the *Os multangulum majus* and *minus*. The third articulates with the *Os capitatum*. The fourth with a very narrow facet on the capitatum and a broad area of the *Os hamatum*. The fifth articulates with the hamatum alone. The *Os centrale* is disc shaped and articulates with and rests in a notch on the distal surface of the navicular bone and by its tight interosseous capsular ligaments forms essentially an integral part of the navicular. When fully isolated the carpus is seen to be curved from side to side with the concavity on the volar surface. The volar rims are formed on the radial side by the *Os navicularis* proximally and the *Os multangulum majus* distally and on the ulnar side by the proximal *Os pisiforme*, which lies wholly on the volar aspect of the carpus, and the distally situated hamulus of the *Os hamatum*. On the volar surface the stout triquetro-lunate ligament forms the basis of the transverse carpal ligament. This extends upward to bind the pisiform firmly in this unit and continues laterally to form the naviculo-lunate ligament.

The distal row of carpal bones is similarly connected by strong volar interosseous ligaments but these are somewhat less distinct than those of the proximal row. Examination of the bases of the metacarpal bones shows them to articulate very closely with one another, and the interlocking articulations between adjacent metacarpals indicates the relative rigidity of this area. The sole exception is the first metacarpal which has no articulation with the second, of the kind noted between the others, and lies in a distinctly volar plane with respect to the base of the second. There is, however, a tubercle on the volar aspect of the base of the second metacarpal and into the groove between this and the base proper, the first metacarpal fits. The connection here, as between the bases of the others on both dorsal and volar aspects, is by stout limiting ligaments.

The *Scapula* is a thin, flat bone, trian-

gular in shape, with a broader thickened inferior axillary margin which forms an acute angle with the medial or vertebral margin. The shorter superior margin joins the vertebral margin almost at right angles, although this posterior superior angle is rounded. The bone is concave on its deep surface which is applied to the posterior thoracic wall. This concave surface presents three ridges running from the vertebral margin and converging on the neck or lateral angle. The dorsal convex surface bears in its upper part the perpendicular *Spina scapulae* which begins some distance from the vertebral margin, sloping upward to its crest and terminating in the acromion process which is directed anteriorly and superiorly overhanging the glenoid fossa. At the neck the bone is thickened and this lateral angle bears on its summit the shallow, ovoid articular surface for the humerus.

Arising from the superior border, near the neck, is the coracoid process. This is thick at the base and directed anteriorly at an obtuse angle, with respect to the superior border. There is a deep notch in the superior border near the base of the coracoid process. In some specimens the posterior tip of the coracoid process, to which is attached the *Ligamentum transversum scapulae superius*, may be partially ossified, almost closing the incisura to form a foramen. The lateral aspect of the coracoid process projects laterally and downward to support the strong origins of the *caput breve M. biceps* and the *M. coracobrachialis* and *M. coracobrachialis profunda*.

The *Spina scapulae* divides the posterior surface into the deep supraspinous fossa and the more shallow but broader infraspinous fossa. The inferior margin of the latter is formed by a prominent ridge of bone which in part overhangs the inferior border. The overhang is more definite as it approaches the lateral angle.

The crest of the spine presents an S-shaped curve, the posterior limb directed superiorly near the vertebral border and the anterior or lateral limb directed inferiorly. In the concavity of the lateral curve is the depression for the origin of the spinous division of the *M. deltoideus*.

The inferior ridge gives a broad area for the origin of the long head of the *M. triceps* and for the *Mm. teres major* and *minor*. This may be described as the *Crista infraglenoidalis*.

The *Cavitas glenoidalis* is on a flattened ovoid prominence with its plane at right angles to the body of the bone, occupying the lateral angle. The very shallow depression has regular margins and is pointed superiorly, being narrowed anteriorly by a groove in which the tendon of the subscapular muscle rests. Above the pointed tip is a facet, the *Tuberositas supraglenoidalis*

for the attachment of the *caput longum* of the *M. biceps*.

The *clavicle* (clavicula) is a short, slender, cylindrical bone with an S-shaped curve. It is divisible into a shaft and two extremities. The clavicle occupies an oblique position on the anterior aspect of the thorax, forming an angle of about 45° with the mid-sagittal line. The shaft is bent convexly forward for almost two-thirds of its length and the convexity backwards is sharper and more acute than the medial curve. The *extremitas sternalis* is broadened and presents a convexity on its anterior aspect which constitutes the roughened surface for the clavicular attachment of the strong sterno-clavicular ligament. The *facies articularis sternalis* is covered with cartilage and consists of a narrow border directed medially. This lies on the curve of the spoon-shaped sternal extremity. The *extremitas acromialis* is somewhat broadened and occupies roughly one-fifth of the length of the bone. It is flattened from above downwards and the under surface presents a rough concave area for the attachment of the coraco-clavicular ligament. The extreme tip of the bone which articulates with the acromion is blunt, and, as noted in the discussion of that joint, occupies a very small and insignificant area. On the convexity of the lateral curve there is a small roughened area to receive the insertion of the *M. subclavius*.

The *Humerus* is a long, cylindrical bone articulating with the scapula above and the radius and ulna below. It presents a shaft or corpus and two extremities. The corpus is distinctly cylindrical above and flattened antero-posteriorly below.

The upper extremity is broadened and supports the *caput humeri* which is hemispherical in shape, the base joining the extremity at an acute angle. The articular surface of the head comprises an area somewhat greater than twice that of the glenoid cavity of the scapula. The *caput humeri* is separated from the shaft by a constricted area, the *collum anatomicum humeri*. On opposite sides this bears the larger lateral *tuberculum majus* and the smaller, medially placed *tuberculum minus*. Between the two there is a deep groove, the *sulcus intertubercularis*. Below, this depression becomes shallower, but in the upper part it is bordered by two crests of bone. The *crista tuberculi majoris* may project or overhang the sulcus in its upper part. This crest may be traced distally to the lower limit of the deltoid surface, in the middle third of the corpus.

The *crista tuberculi minoris*, which is a broad flattened ridge extending downward from the base of the *tuberculum minus*, disappears for a short distance to rise again with a sharper crest for the attachment of the *Mm. latissimus dorsi* and *teres major*.

The *Tuberculum minus* in adult specimens presents a broad flat facet on its medially facing apex for the stout insertion of the *M. subscapularis*.

The *Tuberculum majus* presents three oval facets on its superior surface near the junction with the *collum anatomicum*; the two more lateral ones touching and partially surrounding the medial one. These serve for the insertions of the *Mm. supraspinatus*, *infraspinatus*, and *teres minor* from above downward.

It should be noted that the *crista tuberculi majoris* crowns the summit of an antero-posterior curve of the corpus humeri in its upper third. The apex of this curve, which continues through the greater length of the humerus, lies at the lower point of the insertion of the *M. deltoideus*, in the middle third of the shaft. This is a double curve being from medial to lateral in the middle third of the humerus as well as antero-posterior throughout. The broad flat area extending downward from the *tuberculum majus* serves for the insertion of the deltoid.

The lower extremity of the humerus, consisting largely of the lower third, is flattened from before backward and is much broader than the shaft or the upper extremity. From each side there are rough projections of some size, the medial being considerably more prominent than the lateral. These are the respective epicondyles which give attachment for the ligaments of the joints and for the extensor and flexor groups of muscles of the forearm. Between these lie the articular surfaces of the inferior extremity. This surface bears an oblique relationship to the shaft of the humerus.

The medial of these two surfaces is the roller-shaped *trochlea* which articulates with the *incisura semilunaris* of the ulna. The lateral surface is the rounded *capitulum* with its prominent convexity presenting largely anteriorly. The trochlea, on the contrary, extends around for a considerable area posteriorly.

Above the junction of the trochlea and capitulum anteriorly there is a very shallow depression, the *fossa coronoidea*. Lateral to the latter is the deep rounded *fossa radialis*. The relative depth and development of these is the reverse of conditions in man. This in turn may be related to the greater participation of the radius in the elbow joint. Posteriorly, extending from epicondyle to epicondyle, the *fossa olecrani* occupies the breadth of the inferior extremity.

The *Ulna* is a long, cylindrical bone with a very large, thick, proximal or upper extremity and a long, slender shaft terminating in the small lower extremity or head. The upper extremity articulates with the humerus by means of the deep saddle-shaped *incisura semilunaris* which presents a high proximal crest from the *olecranon*,

and the equally well developed *processus coronoideus* distally. On the lateral aspect of the latter, facing anteriorly and obliquely laterally, is the shallow depression of the *incisura radialis*. The coronoid process shows medially a flaring surface which gives added area for the articulation with the *trochlea humeri*. This flare is definitely more medial than that of the olecranon, which is on a line with the *incisura radialis*. This latter alignment accounts for the fact that the *fossa radialis* and the *fossa olecrani* lie opposite each other on the humerus.

Distally at the base of the coronoid process there is a crest of some size which slopes posteriorly to end on the facies medialis of the ulna. This serves for the insertion of the *M. brachialis*. The olecranon is a roughened stout process of the upper extremity distinctly separated by an appreciable interval from the crest forming the superior lip of the *incisura semilunaris*. Its proximal surface is irregularly flattened for the insertion of the tendons of the triceps complex. Medially there is a separate facet for the insertion of the *M. dorsoepitrochlearis*. The upper extremity of the ulna is flattened from side to side and from the coronoid process to the junction with the middle third is three to four times as wide as the lower part of the shaft. This region is constricted also between the anterior border and the posterior subcutaneous border.

The shaft of the ulna presents a distinct curve with the convexity directed posteriorly. In the lower third, the distal extremity becomes cylindrical and exhibits a prominent crest for the origin of the *M. pronator quadratus*. Below this the bone widens somewhat and terminates in two projections of about equal size, the proximal *capitulum* which articulates by a synostosis with the radius, and the longer distal *processus styloideus* which articulates directly with the concavity of the *Os triquetrum* and to a slight extent with the *Os pisiforme*. The *foramen nutricium* is found proximally on the medial or lateral surface of the flattened area some distance beyond the coronoid process. It is directed proximally.

The *Radius* is a long, slender, cylindrical bone with a prominent well-developed head bearing a shallow circular depression, the *fovea capituli radii*, for its articulation with capitulum humeri. Medially there is a semilunar convex area for the *incisura radialis* of the ulna—this is the *circumferentia articularis*. Just below the capitulum the bone is narrowed to form the *collum radii* and close below this is a rounded projection directed medially, the posterior rim of which serves for the insertion of the flattened tendon of the *M. biceps*. The anterior bulge of this *tuberositas radii* serves as a fulcrum increasing the mechan-

ical efficiency of this insertion. Distal to the tuberosity is the beginning of a laterally directed curve in the shaft which has its convexity in the middle third. To the summit of this curved area the *M. pronator teres* has its broad insertion. The volar surface of the radius is obliquely flattened, sloping posteriorly to the interosseous crest.

The broad lower extremity is flattened in a dorso-ventral plane; the anterior surface serving for the insertion of the *M. pronator quadratus*. The articular surface of the lower extremity faces toward the medial or ulnar side of the arm and bears thus an oblique relation to the shaft of the bone. The *processus styloideus* is a flat projection constituting the lateral border of this articular surface. Medially there is a shallow depression for articulation with the ulna, but as described in the section on the wrist joint this articulation is not by true articular surfaces. Dorsally the distal extremity presents a prominent crest which is broad at its base and separates two deep grooves. The medial one is for the tendons of the *M. extensor digitorum communis*. The lateral groove serves to retain the strong tendons of the *M. abductor carpi radialis* and the *Mm. extensores carpi radialis brevis* and *longus*.

The carpal bones will not be considered individually; they have been discussed in connection with the wrist joint.

The point of chief interest in the phalanges is the striking curve of the proximal phalanges of digits two, three and four, especially. This curve has its convexity dorsally and the volar surface presents a deep groove into which the flexor tendons are tightly bound by the annular ligaments. It is suggested that this great curve increases the mechanical efficiency of the fingers in forming a rigid hook once flexion of the metacarpo-phalangeal joints passes beyond the 90° angle.

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#### EXPLANATION OF THE PLATES.

##### PLATE I.

- Fig. 1. *Lagothrix*. Dissection of shoulder region.

##### PLATE II.

- Fig. 2. *Lagothrix*. Medial aspect of arm and volar surface of forearm.

##### PLATE III.

- Fig. 3. *Lagothrix*. Flexor tendons in carpal canal.  
Fig. 4. *Lagothrix*. Extensor tendons.

##### PLATE IV.

- Fig. 5. *Lagothrix*. Lateral view of metacarpo-phalangeal joint.  
Fig. 6. *Lagothrix*. Superficial muscles of the palm.  
Fig. 7. *Lagothrix*. Extensor tendons and their insertions on the phalanges.  
Fig. 8. *Lagothrix*. Flexor tendons and their insertions on the phalanges.  
Fig. 9. *Lagothrix*. M. flexor digitorum profundus tendons. Volar aspect.

##### PLATE V.

- Fig. 10. *Lagothrix*. Deep muscles of the palm (volar interossei, intrinsic muscles of thumb, index and fifth digit).

Note: The relation of the flexor carpi radialis tendon to its insertion is not clearly shown here. x and y are the os navicularis and os multangulum majus to which the sheath of this tendon is bound. It does not insert on them.

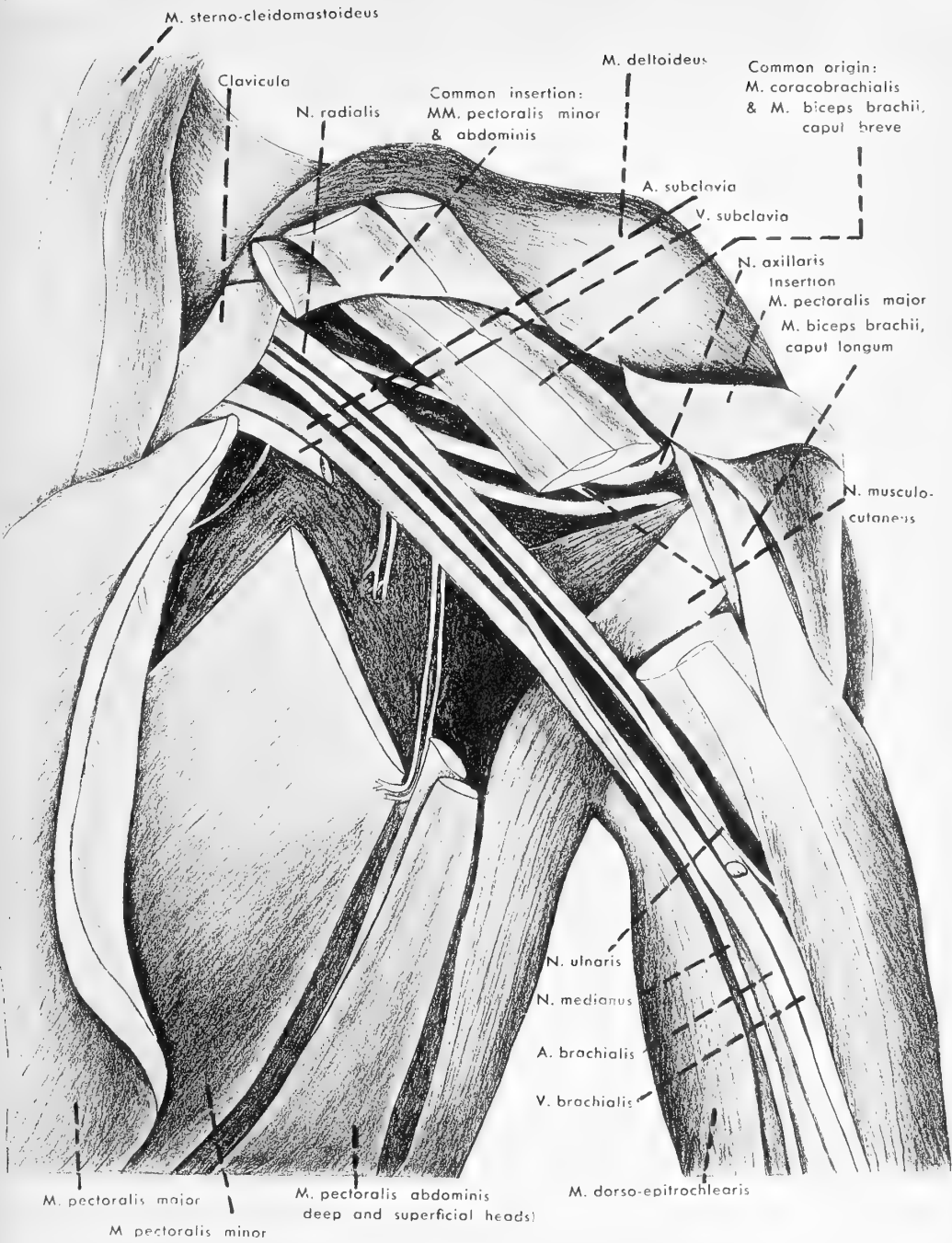


FIG. 1.

ANATOMY OF THE SOUTH AMERICAN WOOLLY MONKEY (*LAGOTHRIX*).  
PART I. THE FORELIMB.



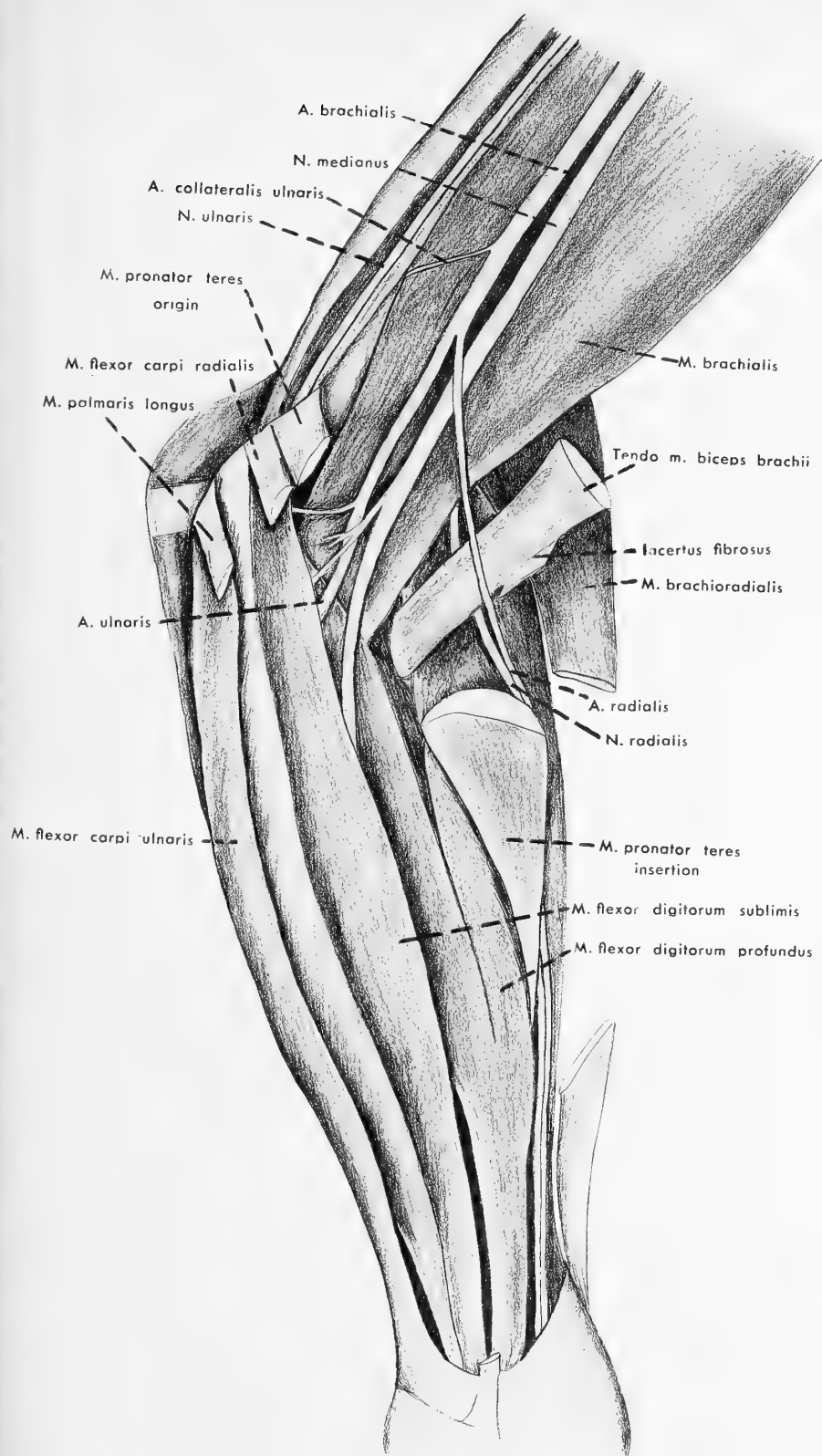


FIG. 2.





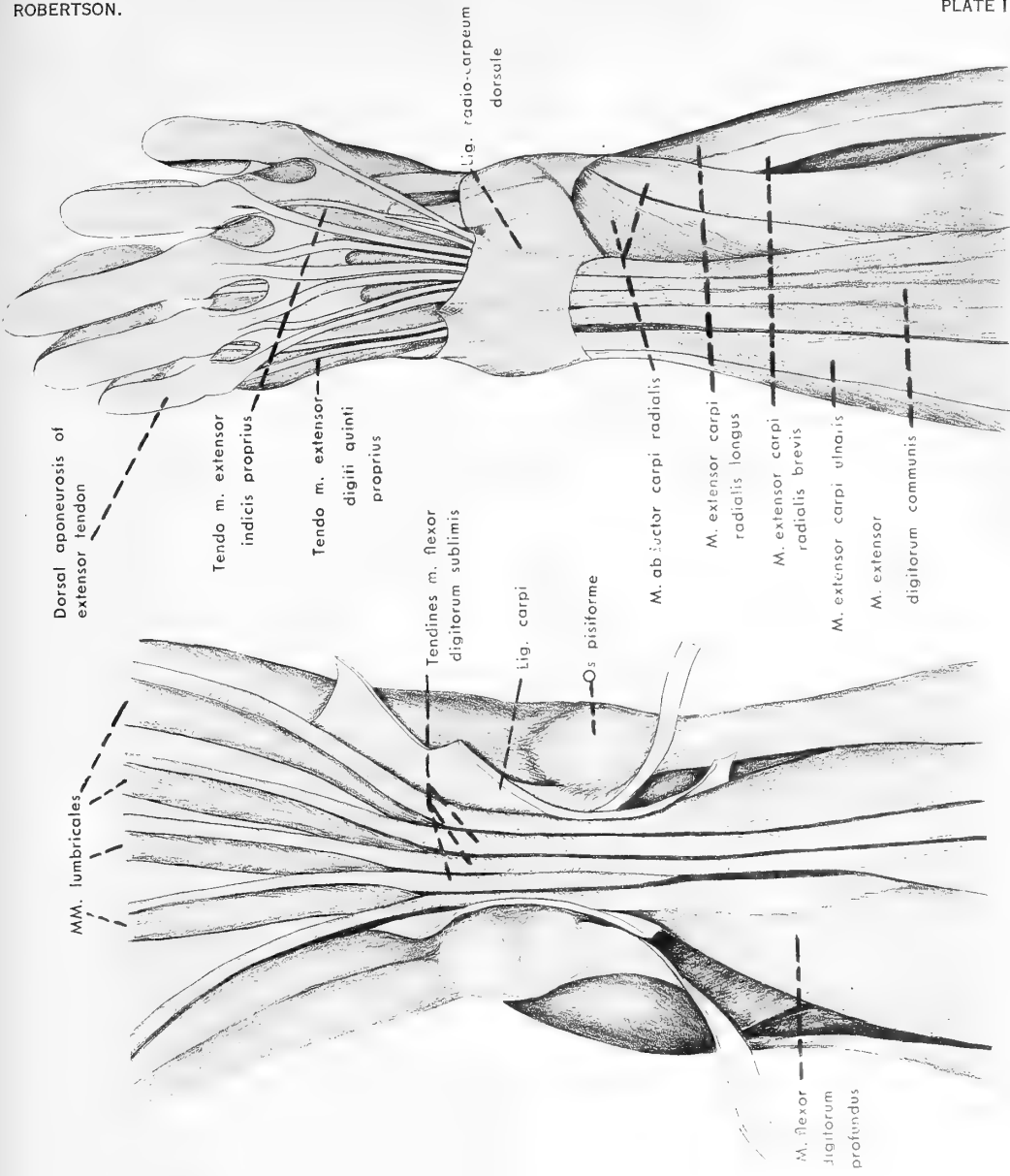


FIG. 3.

FIG. 4.



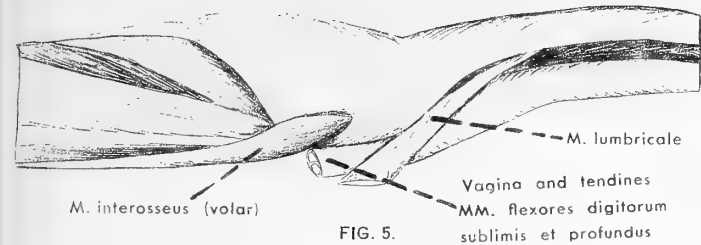


FIG. 5.

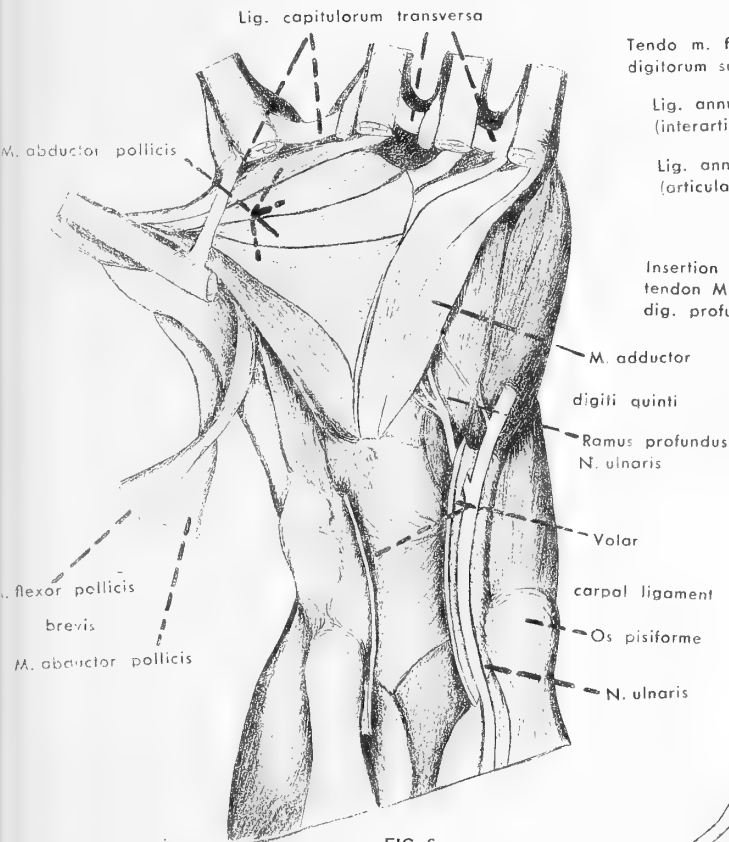


FIG. 6.

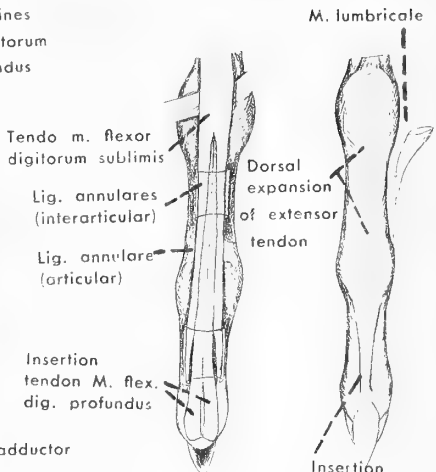


FIG. 7.

FIG. 8.

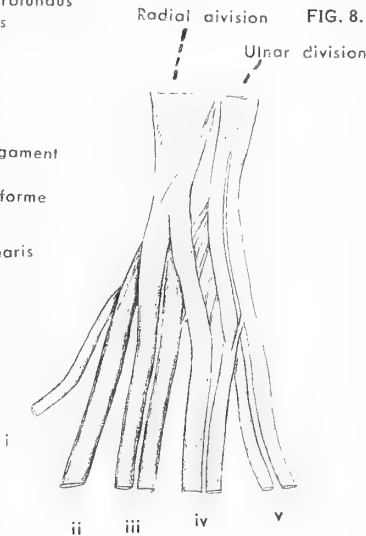


FIG. 9.



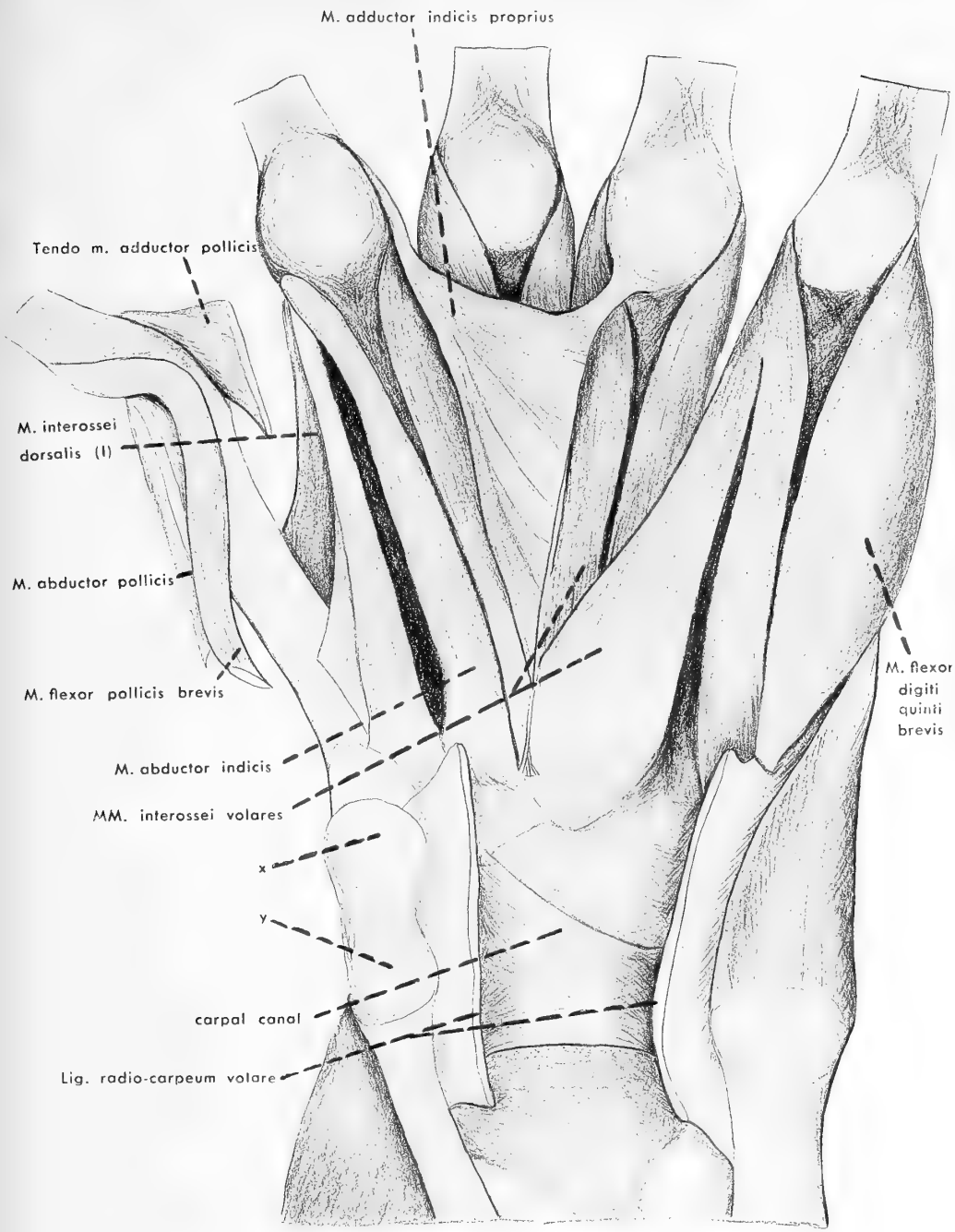


FIG. 10

ANATOMY OF THE SOUTH AMERICAN WOOLLY MONKEY (LAGOTHRIX).  
PART I. THE FORELIMB.



## 17.

Some Venezuelan Membracidae.<sup>1</sup>

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[This is a contribution from the Forty-third or Venezuelan Expedition of the Department of Tropical Research of the New York Zoological Society made under the direction of Dr. William Beebe. The expedition was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

Through the courtesy of Dr. William Beebe, the author has been permitted to examine a small collection of Membracidae from Caripito, Venezuela. The species represented in this collection should be recorded in the literature of the family since fourteen of the eighteen species have never before been reported from that country. The records of Venezuelan Membracidae are very meager and Dr. Beebe's material is valuable in that it furnishes additional information regarding the geographical distribution of the membracids.

The species represented in the collection, together with brief statements of their known general distribution, are as follows:

*Membracis foliata* Linnaeus.

Described from Surinam. Common throughout Central America and northern South America.

*Membracis c-album* Fairmaire.

May be a variety of *M. foliata*. Described from Brazil. Has about the same range as the preceding.

*Membracis lefebvrei* Fairmaire.

Described from French Guiana. Has been reported from Brazil and Mexico but from no other countries. This is the first record from Venezuela.

*Membracis arcuata* DeGeer.

Rather common throughout northern South America but this is the first actual record from Venezuela.

*Membracis tectigera* Olivier.

One of the most abundant species of the genus in tropical America. Is found from Brazil to Mexico.

*Enchophyllum quinque maculatum* Fairmaire.

A rather rare insect which has previously been reported only from Brazil. This is the first record from Venezuela.

*Enchenopa albidorsa* Fairmaire.

Abundant in Brazil, Colombia, British Guiana and occasionally found in Argentina but not previously known from Venezuela.

*Enchenopa lanceolata* Stoll.

Very common over most of Central and South America but not previously recorded from Venezuela.

*Enchenopa serratipes* Buckton.

Formerly considered a variety of *E. albidorsa* but now known to be distinct. A new record of Venezuela.

*Enchenopa ignidorsum* Walker.

Previously known from Mexico, Panama, Ecuador and Dutch Guiana. Apparently not common anywhere. Another new distribution record.

*Campylenchia hastata* Fabricius.

Described from Peru with a general distribution from Brazil to Mexico. Very common in the Canal Zone area but not previously recorded in the literature from Venezuela.

*Spongophorus guerini* Fairmaire.

Another new record from Venezuela but its presence in this country is to be expected since it is quite common in most of northern South America.

*Heteronotus vulnerans* Germar.

A very rare species of the subfamily Darninae which has previously been known only from Brazil and is seldom

<sup>1</sup> Contribution No. 698, Department of Tropical Research, New York Zoological Society.

seen in collections. Dr. Beebe has two specimens. A new record for Venezuela.

*Heteronotus strigosa* Butler.

Another rather uncommon form also recorded in the literature of the family only from Brazil. Another new distribution record.

*Darnis latior* Fowler.

Described from Panama and reported from British Guiana by Haviland and Funkhouser. This is the first record from Venezuela.

*Ceresa vitulus minor* Fowler.

Very common over most of northern South America and extends up through Central America to Mexico and southern United States.

*Cyphonia fuscata* Buckton.

Described from Brazil and known to inhabit Peru and Argentina. This is the first record from Venezuela.

*Stegaspis laevipennis* Fairmaire.

Known in the literature from Brazil, British Guiana, Peru and Colombia. Not previously known from Venezuela.



## 18.

Field Notes on the Lizards  
of Kartabo, British Guiana, and Caripito, Venezuela.  
Part 2. Iguanidae.<sup>1</sup>

WILLIAM BEEBE.

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New York Zoological Society.*

(Plates I-VI; Text-figures 1-17).

[This contribution is a result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana and to Venezuela, all made under the direction of Dr. William Beebe. The Guiana expeditions were made during the years 1909, 1916, 1917, 1919, 1920, 1921, 1922, 1924 and 1926, and the Venezuelan trips in 1908 and 1942. The latter was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

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INTRODUCTION.

This is a second paper on the lizards of Kartabo, British Guiana, and Caripito, Venezuela.<sup>2</sup> In the year 1909, and from 1916 to 1928, eight expeditions were sent out from this department to British Guiana, and in 1908 and again in 1942 field work was carried on in Venezuela.

Throughout the course of these expeditions many field notes, color plates and photographs were made of tropical vertebrates, and the object of this present series

is to assemble and publish some of these notes and illustrative material. Any change or alteration of the original notes is placed between brackets. The chief value of these data is that they are concerned with living or freshly killed specimens.

The observations in Guiana were made in one-quarter of a square mile of jungle at Kartabo, and those in Venezuela at or close to Caripito, which is only 528 kilometers northwest of Kartabo.

In addition to numerous technical papers in *Zoologica* and several popular volumes, there have been published the following general ecological summaries: *Zoologica*: (Kartabo) Vol. II, No. 7, 1919, pp. 205-227; Vol. VI, No. 1, 1925, pp. 1-193. (Caripito) Vol. XXVIII, No. 9, 1943, pp. 53-59. Also see "Tropical Wild Life in British Guiana" by Beebe, Hartley and Howes, published by the New York Zoological Society, 1917, pp. 1-504.

My hearty thanks go to Dr. Charles M. Bogert of the American Museum of Natural History and Dr. Karl P. Schmidt of the Chicago Natural History Museum for identifications and for bringing up to date my often out-worn names of many years ago.

My original field numbers and other data have been appended to descriptions, breeding and other notes. These specimens are either in the collections of the Department of Tropical Research or in those of the American Museum. Whenever the term total length is used, a perfect, unregenerated tail is understood. Many of the figures in the plates are black and white reproductions of original colored paintings, so only the pattern is preserved. The following are from paintings by Isabel Cooper, Plate-figures 1, 2, 3, 7, 9, 10, 17 and 18. Text-figures 3, 7, 11, 12 and 16. From drawings by George Swanson, Plate-figures 11 and 19. Text-figures 1, 4, 5, 8, 9, 13, 15 and 17. From photographs by T. V. Smolucha, Plate-figures 4, 5, 6, 8, 14, 15 and 16.

<sup>1</sup> Contribution No. 699, Department of Tropical Research, New York Zoological Society.

<sup>2</sup> Part 1, Gekkonidae, *Zoologica*, Vol. 29: pp. 145-160.

### FAMILY IGUANIDAE.

**Ecology of the Genera:** Seven genera and fifteen species of this family of lizards were found at Kartabo, British Guiana, only four of which were recorded from Caripito, Venezuela. A longer period of field work at the latter locality would doubtless reveal many of the others. Eight of the fifteen species belong to the genus *Anolis*, which is not surprising when we recall that about one hundred species of these little lizards range from North Carolina to Brazil. Only two other *Anolis*, *lentiginosus* and *longicrus*, have been recorded from "The Guianas," neither of which we encountered. The *Iguana* we found is the only species of its genus, ranging in several subspecies over Central America, the West Indies and the northern half of South America. *Plica* is represented by two out of the four known species, the two remaining forms inhabiting Bolivia and Argentina respectively. *Polychrus* is present in one out of the two species of the genus. A single species of *Tropidurus* was found out of the twenty-odd known from elsewhere. *Uranoscodon* is a monospecific genus, confined to north-eastern South America. Out of six known species, one species of *Urocentron* was collected. This had hitherto been recorded only from Brazil.

**Occurrence:** In order of relative numbers as observed by us, we have: abundant, *Anolis*; common, *Iguana*, *Plica* and *Polychrus*; occasional, *Uranoscodon*; rare, *Tropidurus* (4) and *Urocentron* (2).

**Size:** From small to large; *Urocentron* (average 100 mm.), *Tropidurus* (150 mm.), *Anolis* (175 mm.), *Plica* (310 mm.), *Uranoscodon* (360 mm.), *Polychrus* (450 mm.), and *Iguana* (up to 1200 mm.).

**Food:** *Iguana* appears to be strictly vegetarian, but all the other lizards feed on insects and other invertebrates. Hints of cannibalism are observed rarely, and a small but definite amount of vegetable matter is taken by *Polychrus*.

**Eggs:** The number of eggs recorded is as follows: *Anolis* 2 (which may be deposited simultaneously or a week apart); *Plica* 2; *Iguana* 4 to 7; *Polychrus* 7 to 8; *Uranoscodon* 6 to 11.

**Habitat:** All fifteen species, with the exception of *Urocentron*, are essentially arboreal. *Anolis* and *Iguana* are found occasionally on the jungle floor, and the latter breeds in subterranean burrows. Among anolids fairly distinct haunts may be differentiated. *Anolis aeneus* and *fusco-auratus* are at home on low and rather small tree trunks, the latter preferring those with pale, lichen-covered bark. *Anolis biporcatus*, *chrysolepis* and *nitens* by preference choose the foliage of low jungle growths, and *Anolis punctatus* is found usually on the ground.

**Escape Methods:** Even the smallest anolids, when once seized, will bite ferociously but futilely, as their teeth are too minute to puncture human skin. The bite of a large iguana is very different, as the powerful muscles and sharp teeth can make an ugly wound.

All iguanid lizards, however, strive to escape observation by immobility, plus confusing postures and more or less swift change of pattern and coloring. *Anolis nitens* trusts so completely to its protective pattern that it can usually be picked up in the hand. *Plica* rests upsidedown on self-colored tree-trunks, and *Polychrus* assumes strained positions and holds them for hours, at the last moment rushing off headlong and again assuming a posture which allies it more to twigs and tendrils than to a living saurian. In *Uranoscodon* this trust is carried to an extreme, and not only can these lizards be picked from their perch on a tree, but carried home in what appears to be a trance-like condition. Once awakened from this, the phenomenon may reoccur from time to time in captivity. Iguanas feed usually high up in trees, and their favorite method of escape is to fling themselves headlong into water far beneath, or to flatten out and crash unharmed into thick foliage near the ground.

**Competitors:** As far as insect food is concerned, the only vertebrate competitors of the iguanid lizards are toads, brevicipitids and ant-thrushes on the ground, tree-frogs and low living jungle birds in low foliage. The tree-trunks are shared with dendrocolaptine birds.

**Enemies:** Snakes are the source of greatest danger to these lizards, with jungle hawks a close second. Birds belonging to the genus *Attila* of the jungle cotingas feed extensively on small lizards, as do some of the terrestrial ant-thrushes. At Caripito, Mr. Swanson of my staff saw a good-sized jaguar in full pursuit of a large iguana, crossing the trail only a few yards away.

### *Anolis aeneus* Gray, 1840.

**Name:** Marbled *Anolis*.

**Range:** British Guiana, Venezuela, Trinidad and Tobago.

**General Account:** More than any other anolid, this species is semi-gregarious, occurring in limited areas of the jungle in relatively large numbers. I have found eleven in a space of ten square yards and no others anywhere nearby, although there was no apparent change of plant growth or of elevation. The marbled anolis is a tree-trunk lizard like *Plica*, rather than a frequenter of low, leafy bushes. I have seen and shot them at a height of thirty-five feet on the trunk of a mora.

In general, the head and neck are grayish. Body, limbs and tail buffy brown, indistinct-

ly mottled, banded and striped with darker. Beneath, head, throat, legs and terminal two-thirds of tail whitish; body and basal third of tail pale lemon yellow.

Two males displaying before females well up on the trunks of trees exhibited unusually extensive dewlaps. They began half way between the eye and tip of the snout and extended down the ventral surface half-way between the insertions of the fore and hind limbs. The vertical breadth was large in proportion.

There is no symmetry of dorsal markings, the pattern being of irregular blotches and reticulations, and I have noticed very little change in day and night alteration of color.

The tail is exceedingly deciduous and it is difficult to secure a perfect specimen. In two individuals shot from trees, the tail was freshly lost in one and semi-detached in the other, not from a shot injury. It is probable that this occurred from the shock of striking leaves or foliage in the fall of the anolis to the ground. I have never seen any hint of the lizard being able, by its own exertion, to discard its tail. Locally it is fairly common at Kartabo but I did not take it at Caripito. A blue-tinged individual was captured at the pitch lake at Guanoco, a few miles down river from Caripito.

In my journal I find references to detailed observations on this species but the notes themselves have disappeared.

**Food:** A specimen taken March 10, 1919, had its stomach filled with more than seventy-five mosquitoes, and another anolis had devoured fifteen termites.

#### ***Anolis biporcatus* (Wiegmann, 1834).**

**Name:** Brown-backed Anolis.

**Range:** "Western Ecuador, northward into Central America," British Guiana.

**General Account:** Only two specimens were taken at Kartabo. Color Plate 1171 is of Specimen 204, a female, total length 160 mm., April 22, 1919. This individual is mottled with several shades of gray, and from the nape back to half-way down the tail extends a wide, vertebral band of light olive-buff. The dewlap of the second specimen, a male, when distended showed no heightened color, just a grayish-white expanse of skin. Both geckos were taken in one sweep of a butterfly net as they rested on the leaves of a low bush in the jungle.

These were identified by Dr. Noble; one specimen given to the American Museum, the other to the museum at Georgetown, British Guiana.

#### ***Anolis chrysolepis* Dumeril and Bibron, 1837.** (Plate I, Figs. 1 and 4).

**Names:** Vertebral-striped Anolis, Gold-striped Anolis, Large Jungle Anolis.

**Range:** Venezuela, Trinidad, the Guianas and Brazil.

**General Account:** This is the second in abundance of Kartabo and Caripito anolids, the first being *Anolis nitens*. Their favorite haunts are the leaves of low shrubs and bushes in the jungle and along the streams.

**Female breeding,** No. 2836, Kartabo, May 14, 1924, Color Plates 737, 738:

**Measurements:** Total length 136 mm. Following are percentages of length: Head 10.3 per cent., head and body 36, tail 64, head width 5, fore leg 13, hind leg 27, eye diameter 1.4 per cent. Weight 1.5 grams.

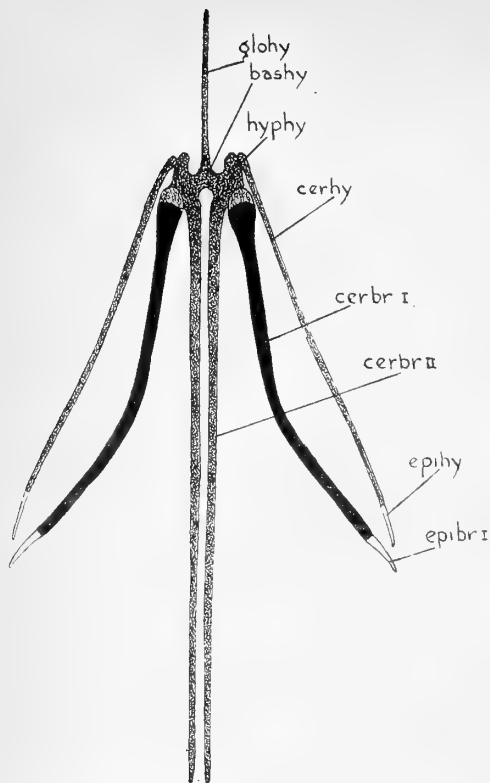
**Color in Life:** General color above olive with a strong greenish-yellow tinge. A double, broken, backward pointing, V-shaped, dark brown mark between the eyes. Starting the same distance from the pineal scale as its distance behind the point of the ocular V-mark is a broad dorsal stripe of yellow ochre, overlaid with two narrow stripes, one on each side of a light golden. There is a fine line of the yellow ochre outside of these gold stripes on each side, then a broad edging of very dark brown, black on the inner side and fraying out to an irregular scattering of sepia freckles. Sides of head and body and upper parts of limbs are faintly spotted with red brown. Laterally and along sides of neck and chin are strong mottlings of lavender which die out to purest white on the chin, small dewlap and ventral surface. This latter is immaculate except for scattered specks of very light brown posteriorly and for a dull brown tinge to the under surfaces of the limbs. Tail is faintly barred with narrow rings of brown, becoming mottled half way down and finally black on the last quarter inch. Pupil ring gold; iris orange with faint dark mottlings.

**Male not breeding:** Above brownish-black, with wide median stripe of burnt orange variegated with gray. A broad band across top of head between eyes. Below grayish-white, with scarlet dewlap. Iris dark brown with inner ring of gold.

**Male not breeding:** Back dark olive buff shading downward to wood brown and pinkish-white on ventral surface. Dorsal stripe pale vinaceous bordered with natal brown. Head mottled with various shades of brown with broad eye band of olive. Face sandy shading to wood brown on snout. Irregular light markings near eye and one wide golden band from eye down and back to jaw. Legs and tail buffy brown with mottlings of darker.

**Female breeding:** Black inter-orbital stripe edged with lighter. Vertebral stripe orange.

**Male not breeding:** Mottled grayish-olive above with broad vertebral stripe of yellow buff, bordered with black. Mottled white below. At death darkens, the back stripe be-

TEXT-FIG. 1. *Anolis chrysolepis*. Hyoid.

coming bright gold anteriorly, reddish-brown on tail.

Female breeding: General color smoke gray with fine black stippling. Snout lighter. Top of orbits bright yellow gray, with hour-glass transverse marking of dusky. Dorsal stripe olive buff, lighter on lower back and tail. This stripe narrows over the shoulders and widens on lower back. Sides of face buff mottled with brown. Limbs smoke gray mottled with black. Ventral surface vinaceous with dark mottling under limbs and tail. Iris apricot yellow with fine freckling.

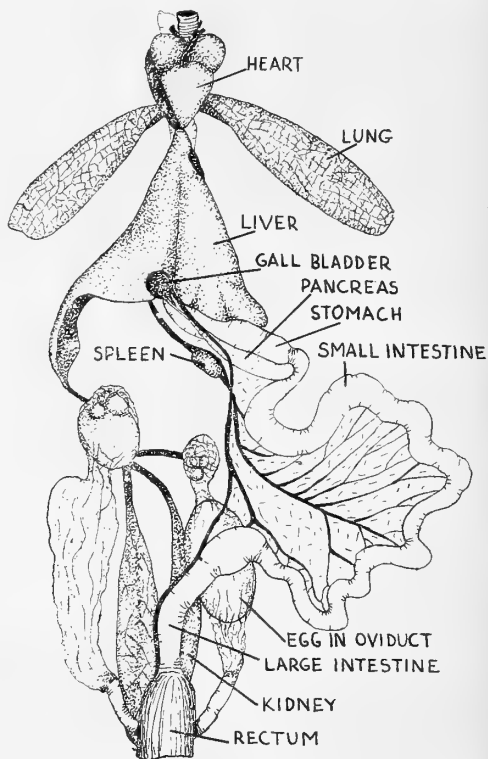
These six descriptions will give an idea of the infinite variation. Often an anolis will change so radically that a description cannot be finished, some characters vanishing or being complicated by others. The two main differentiations into dorsal striped and no dorsal striped is regardless of age or sex. In the preserved specimens, flank markings and the eye band often remain the most distinct.

In a series of delicate measurements it was found that within a week, the change in total length from the living or just dead to the same specimen preserved, was from 1 to 3 mm.

*Hyoid*: Coll. No. 30,083, Caripito, April 10, 1942, adult male, total length 210 mm. Text-fig. 1. The glossohyal is an extremely

attenuated, needle-like element, equal in diameter throughout, extending forward 3.5 mm. from the basihyals. The latter are rather unlike their usual arch-like shape, due to amalgamation with the hypohyals. These latter are distinguishable as short, thick, forward-directed shoulders, completely ossified with the basihyals. From the anterior tips of these shoulders arise the ceratohyals, externally and with no evidence of a socket, as slender as the glossohyals, 8.5 mm. in length and directed at an acute backward angle. Short, transparent, distal tips represent the remains of epihyals.

From the thickened, posterior shoulders of the basihypohyals spring the first ceratobranchials, their enlarged, rounded proximal caps fitting nicely into deep, almost quarter-circle, concave sockets. These elements consist of dense, osseous-like tissue and their decided curve in another plane gives, from the dorsal aspect, a false impression of a rather sharp angle at mid-length. They are the heaviest elements in the entire hyoidean complex, and support the usual short, distal vestiges of first epibranchials. The second epibranchials surpass in development even those in *Polychrus*, being twenty-five per cent. longer than the ceratohyals. They arise as posterior, ankylosed continuations of the basihyals, extending straight backward 12 mm., decreasing slightly in caliber.

TEXT-FIG. 2. *Anolis chrysolepis*. Gross anatomy.

**Food:** The food of the gold-striped anolis did not show much variation. In order of abundance eaten, the five major ingredients were termites, spiders, ants, roaches and grasshopper nymphs.

**Breeding:** As marked by courtship and the deposition of eggs the following months were noted in my journal: March (2 times), April (1), May (3), June (7) and August (2 times).

An average egg measures 7 by 13.5 mm., the largest one 8 by 16 mm. The average weight was 2.8 grams. Dissection showed that 2 eggs might be laid simultaneously, but usually the second was several days to a week behind the first in developmental stage. The shell of the egg was rough, with numerous longitudinal striations or furrows. If not kept away from nest debris the egg became densely coated with whatever it touched within the first half hour after being laid.

***Anolis fusco-auratus* D'Orbigny, 1837.**

**Names:** Plain Jungle Anolis, Lichen-colored Anolis, Tree Anolis, Clay-colored Anolis, Snub-nosed Anolis.

**Range:** Northern South America.

**General Account:** Next to *Anolis chrysolepis* and *nitens* this is the most abundant anolid at Kartabo. It is decidedly a tree, not a bush or ground, lizard and is almost always found on pale bark or that encrusted with light-hued lichens. This choice of habitat is very pronounced and observable day after day. The immediate reaction toward an intruder is for the lizard to scurry up the trunk, so it was often necessary to shoot the reptiles with fine shot in order to obtain them. I never saw one on the ground and only once away from a good-sized tree. Specimens No. 698 and 699 were captured among the topmost foliage of a ninety-foot tree within fifteen minutes after it had been cut down. The tree fell in an open secondary clearing, so it may be assumed that this pair of arboreal anolids was living at a great height.

**Color in Life:** In addition to emotional and illumination color changes there are general types of patterning, one pale buffy with many irregular elongate spots and blotches, the other darker with a series of small, dark, mid-dorsal, roundish spots. Females usually show the latter tendency, but I have seen males in full breeding condition with both patterns well developed. Also the dewlap may be dominantly yellow or with much of the central area bright scarlet.

Adult male, pale phase, No. 2823, total length 130 mm., Color Plates 728, 729, 730, May 8, 1924: General body color pale smoke gray. Head and neck blotched with lightish gray (the only color in Ridgway that approximates this is light mineral gray). Body

has scattered, broken, lateral streakings of red brown and a broken, very vague line across the orbits of hair brown. Eyelids light vinaceous, limbs tinged with russet. Dewlap amber yellow, lighter toward median line; scales of lower neck becoming russet vinaceous as they spread out over the dewlap. Ventral surface dull yellowish-white, pinkish under arms, immaculate except for the chin region which is marbled with light brownish. The body color shades to white on the posterior two-thirds of tail, which has ten wide bands of deep brown, separated by twice their length of ground color, and becoming blacker toward tail tip. Pupil rim brilliant gold, iris orange, flecked with gold.

The dark phase of the same individual has the whole body clouded with sepia, the limbs darkening to uniform brown.

Breeding male, dark phase, No. 248, total length 145 mm., Color Plate 285, December 31, 1920: General color olive buff, with dull red brown head markings and broad tail bands. Fourteen small, irregularly rounded dark spots down the back from nape to beyond posteriorly adpressed knee. Ventral surfaces whitish. Dewlap pale chalcedony yellow at top, white front and back with large rounded patch of bright coral pink in center, the lines of scales over its expanded surface conspicuously white. The dewlap is large, extending from the vertical of anterior orbit, back to the line of adpressed elbow.

Male, not breeding, dark phase, No. 542, total length 90 mm., April 18, 1922: General color buffy olive, sides of face, neck and body olive, faintly mottled with cream buff. Chin and throat pallid with sparse brown stippling, moderately developed dewlap white anteriorly, in general coral pink with tinge of cream in center. Median gular scales of dewlap white. Iris brilliant gold mottled with darker.

Adult male and female, Nos. 698 and 699, total lengths 134 and 135 mm., weights male 1.1, female 1.6 grams: Caught in fallen tree-top foliage, August 9, 1922. Both in dark phase, ground color grayish-olive, darker mottlings along mid-back, others on head and snout. Limbs and feet fuscous. Tail marked alternately with fuscous and olive. Extreme body changes range from dark gray to dull green. Throughout these changes the male is paler, especially on head and tail. This makes the dorsal marks and the caudal bands much more distinct. The most radical difference between the sexes is the dewlap, which is almost absent in the female, represented by only a self-colored, slight throat fold. In the male it is relatively enormous, 20 mm. long by 10 high, extending from below the anterior level of the eye to the mid-belly. Elsewhere the male is uniform in ventral coloring, white on chin and throat, buffy white on body and base of tail.

The female is white below, much marbled with dark brown along the line of the jaw and down the center of the body.

**Breeding:** Breeding males were found on May 10 and 16, August 9 and December 31. A female taken on May 12 contained an egg about to be laid, measuring 5 by 10 mm., and another egg with well developed yolk which would have been ready in ten more days.

***Anolis nitens* (Wagler, 1830).**

(Plate I, Figs. 3 and 4).

**Names:** Oblique-striped Anolis. Ho-kobee, Ey-a-moo-ru (Akawai Indian).

**Range:** Northeastern South America.

**General Account:** The most abundant anolis both at Kartabo and Caripito also exhibits the greatest variation in coloration but not in pattern. It is found in the jungle both on tree trunks and on low bushes, but usually on the latter.

Two general types of coloration are found, the lizards with dominant brown and honey yellow markings, and those with black, gray and white. The most persistent character is the pink rump which is almost invariably present both in the lightest and darkest phases and in both sexes. It vanishes very soon after death.

The most characteristic pattern is a series of posteriorly pointed V-shaped markings on the back from shoulder to beyond the base of the tail, accounting for my long-used field name of oblique-striped anolid. These alternating V's may be black, buff, honey yellow, gray or brown. The head is variously striped and banded with contrasting colors, and always with a large orange or white stripe from eye to ear, and alternating bands along the edge of the lower jaw. The limbs and tail are banded with more or less regularity and the under parts are pale yellow, light gray or white. The dewlap, when well developed, is invariably scarlet, with a whitish base and dark, widely spaced scales over the expanded surface.

There is little distinction in the relative size of the sexes. In 12 breeding males, all with perfect tails, and with extreme total lengths of 166 to 209 mm., the average was 186 mm. In six breeding females, measuring from 165 to 198, the average was 180 mm.

This anolis has more confidence in its protective coloring than any other species and it is not difficult to pick an individual from leaf or trunk. The hand must be moved very

slowly, and a more certain method is to wriggle the fingers of one hand in front of the lizard while the other approaches from above or behind. In neither case is there any chance of not being observed. The bright eyes of the anolis watch keenly, but in the divided interest the capture is more certain. It is remarkable how the lizard will watch the fingers actually close on its body without moving. The least jerk or quick motion will send the creature away in a lightning dart.

**Food:** The food of fifteen individual anolids was as follows: termites (occurring 12 times), grasshopper nymphs (10 times, all in April), beetles (5), ants (4), roaches (4), caterpillars (2), spiders (2), the anolid's own skin (2), mole cricket (1).

**Breeding:** I find records for only a portion of the year at Kartabo, for breeding of this species. This, of course, is only a part of the whole picture. April (13 records), May (9), June (5 records), July (2) and August (2 records).

An average egg measures 8 by 16 mm., and is rough in texture with numerous longitudinal striations. Usually a single one is deposited but in one female I found two eggs almost ready for laying, measuring respectively 13 and 14 mm. in length.

A full-grown female kept in a vivarium ate 114 termite workers in 11 days, and probably many more when I was not watching. When a choice of other food was offered, the termites were always taken first. After a two-day fast, the lizard ate a yellow and black hemipteron which would be called warningly colored. On five succeeding days eight other insects of the same species were refused on sight without any attempt at tasting. After another two days' fast she refused a very small *Dendrobates trivittatus* and when the juices of one of these frogs was rubbed on a grasshopper nymph the anolis rejected the grasshopper after taking it in her mouth.

***Anolis punctatus* Daudin, 1802.**

**Names:** Blue-spotted Green Anolis, Large Pug-nosed Anolis.

**Range:** Northern South America.

**General Account:** This species seems rather rare, only three specimens being seen and taken at Kartabo and none at Caripito. One is No. 3129 (21293 in American Museum), Kartabo, 1919, total length 195 mm. The second, No. 3269, male, total length 250 mm., September 1, 1920. Both of these lizards were taken on leaves on the ground in the jungle.

Male adult, No. 3024, Kartabo, August 30, 1920, Color Plate 219:

**Measurements:** Length 220 mm., head 11 per cent. of length, body 39, tail 50, fore leg 15, hind leg 24 per cent., weight 7.4 grams.

**Color in Life:** This male is essentially



dark yellow green including all upper parts, head, body, limbs and toes, with a sparse scattering of small, irregularly rounded spots of pale turquoise blue, largest on the sides of body. The middle third of the tail is brilliant neva green, and the terminal third vandyke brown. Dorsal head scales are touched with bright chalcedony yellow and orange. Sides of head anteriorly green, scales below the eye shaded with primuline yellow; eyelids russet vinaceous with a double row of yellow scales around the eye. The dewlap is very large, beginning at the vertical in front of the eye and reaching back almost to mid-abdomen. Its depth is considerably more than from the posterior eye to tip of snout. It is distinctly but not brilliantly patterned and colored cadmium yellow, and when widely distended 10 or 12 rows of separate scales show as curved lines of white dashes, those in the central rows flanked with black at the bases.

**Color Change and Habits:** The blue-spotted anolis has considerable power of color change, and both dorsal and ventral greens, under stress of emotional excitement, become varying shades of russet and terracotta. When chloroformed it becomes in general brown with the pale spots turtle green, and below dull brownish. The dewlap remains unchanged except that it darkens in general. An hour after death, in two instances, the normal green colors of life returned until placed in preservative. In preservative this anolis turns black or dark wine color, all trace of the green and blue disappearing.

Unlike the more common anolids this seems unadapted to captivity and refuses to feed readily. In the first excrement pellet were the remains of two winged queens of *Cryptocoris atratus*. It was seen to feed on termites.

***Anolis sagrei* Cocteau, 1837.**

**Range:** Northern South America, north to Honduras; Cuba.

**General Account:** I have records of only five specimens taken at Kartabo, two of which (21272 and 38675) are in the American Museum.

Usually dark gray with a series of thin V-shaped lines down the back. These marks are sometimes more or less broken up into spots and blotches on a dull greenish background. This general color can shift to a reddish-brown.

A female, No. 193a, secured August 10, 1919, laid an egg a few minutes after being placed in a vivarium. I can find no further notes in my journal.

***Anolis schiedii* (Wiegmann, 1834).**

**Name:** Small Brown Anolis.

**Range:** Northern South America.

**General Account:** Only one specimen re-

corded from Kartabo. No. 3119, September 6, 1919. Length head and body 40 mm. (tail broken). In my field notes not distinguished from other anolids.

The type of *gibbiceps*, a synonym (named by Cope in 1864) was taken at Caracas, and measured 49 mm. from snout to vent. The color description given by Boulenger (Catalogue of Lizards British Museum, Vol. II, p. 52) is as follows:

"Coppery above, uniform; sometimes with darker spots, or a light vertebral line in the female; lower surfaces whitish with metallic gloss."

***Iguana iguana iguana* (Linnaeus, 1758).**

(Plate II, Figs. 5 and 6. Plate III, Figs. 7 and 8)

**Names:** Iguana. Kuana (Boviander). Why-ah-mah-kah (Akawai Indian, "one who lives in the bush").

**Range:** Northern South America with other forms in Central America and the West Indies.

**General Account:** The iguana is the largest and most generally distributed of the lizards in the two districts under consideration. It is a vegetarian, essentially arboreal and seldom seen on the ground. While it can be considered a green lizard, yet its frequent banding with brown and its power of both pattern and color change make it very difficult to describe in general.

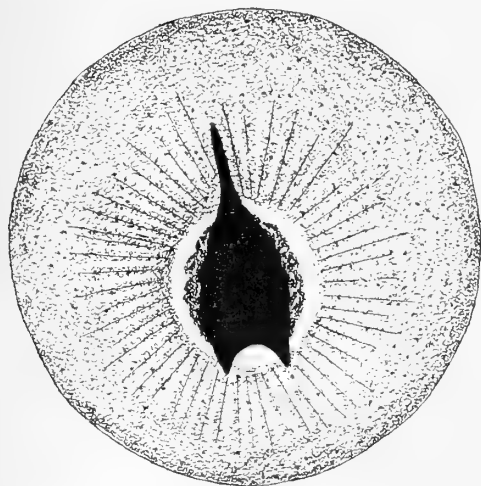
A typical individual is an adult female No. 2877, Kartabo, June 3, 1924, Color Plates 754 and 755:

**Measurements:** Total length 635 mm., head 6 per cent. of length, body 34, tail 60, fore leg 15.7, hind leg 24.5 per cent., weight 249 grams.

**Color in Life:** General color above grayish-olive with wide wash markings, generally pointing backward, of bluish-green with interspaces black variegated with small spots of light grayish-olive. A few of the lateral patches are vivid green and there are four very irregular, rectangular areas, edged posteriorly with black, of pale yellow green with dark stippling. The neck region has a black-edged cape of teagreen, fading to pale olive along its scalloped rear edge, which extends from the beginning of the vertical crest of spines on the nape, to a point a little back of the armpit. This cape is streaked and mottled with black and merges into the olive buff of the dewlap and the faintly bluish-green and pinkish scales of the head. The dewlap is marked with several almost vertical streaks of dark gray. Top of head strongly tinged with olive. A patch of black behind the orbit and one just below it, also a streak of blue green along the gape. The spines of the dewlap are buff, and there is a shade of wine color along the lower edge of this structure. The large cheek

scale is pale green with a patch of pink. Tympanum apricot yellow. Ventral surfaces pale green along the middle, olive buff on each side. Under limbs olive buff, mottled with darker. Fingers and three inner toes bright green. Limbs very dark brown with faint water markings of green, thickly sprinkled with olive. Iris cinnamon rufous tinged with dark brown and an inner gold ring.

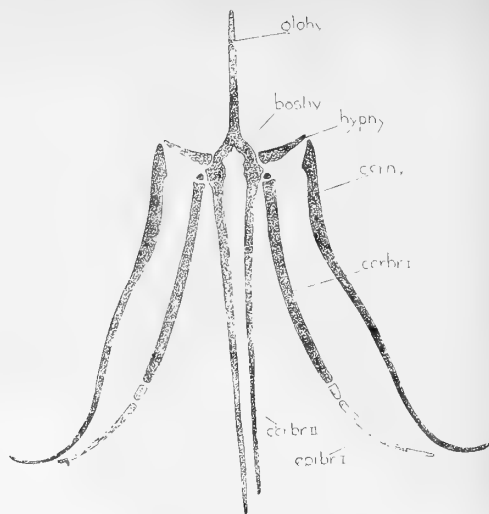
A young iguana of 200 mm. showed a simple pattern of general brilliant grass green above with five irregular bands of dark brown around the body and six around basal third of tail. The caudal rings shaded backward from deep green to pale blue green.



TEXT-FIG. 3. *Iguana iguana*. Fundus Oculi.

*Fundus oculi*: The eye of female No. 2877 was examined and described by Dr. Casey Wood and Mabel Satterlee on the day the lizard was caught, June 3, 1924, Text-fig. 3. Eyeground gray with darker stipples covering the entire fundus. The optic nerve is a rough circle almost entirely covered by the pecten. It is white and has white opaque nerve fibres radiating from it into the surrounding fundus. The pecten is dark brown, almost black. Its base is fairly circular with uneven edges, but the lower end is prolonged in two little swallow-tail points. It comes up into a high point which overhangs the optic at the upper edge for quite a distance. White opaque nerve fibres radiate from the papilla and there are dark brownish lines interspersed between them.

*Hyoid*: Coll. No. 3128, Kartabo, half-grown male, July 4, 1920, total length 635 mm., Text-fig. 4. The glossohyal extends forward as a slender rod, of equal diameter throughout its length of 8.2 mm. At its proximal end, it enlarges into the basihyals, which form an arch of only slightly greater



TEXT-FIG. 4. *Iguana iguana*. Dorsal view of Hyoid.

diameter, and which is given an artistic touch by two scallops, evident both on the outside and on the inside of the arch. Their practical use is apparent on the outside where these indentations act as sockets from which arise the proximal elements of the hyoid and the first branchial arches.

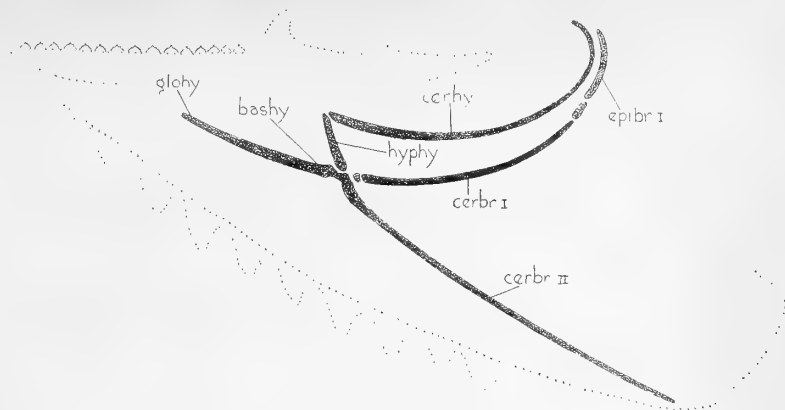
From the anterior facet spring the hypohyals, 3.3 mm., in length, ossified wedges, diminishing slightly in diameter and directed slightly anteriorly. From their tips, the very long, slender and somewhat curved ceratohyals extend backward at a sharp angle from the hypohyals, each 25 mm. in length. Although the tips are very attenuated and curved I can detect no differentiation into distal epihyals.

From the posterior, basihyal, concave sockets arise the pair of first ceratobranchials, each 15 mm. in length. The juncture is by a rounded hyaline cap within which is an ossified core. These elements are slightly greater in diameter than the ceratohyals, and are directed along a closely similar course. Continuing from the distal ends of the first ceratobranchials, are two consecutive elements, the first very short, 1 mm., and the end portion, 7.5 mm., long, slender and curved. If this condition was present in only one of the ceratobranchials, I should consider it an abnormal break, but it is identical in both. I believe the short intercalated rectangle is of the nature of a connecting element of use in providing increased mobility, and the longer, curved distal element as the first epibranchial.

The second ceratobranchial arises as posterior, undifferentiated extensions of the basihyal arms, well separated proximally, and only slightly nearer one another at their



TEXT-FIG. 5. *Iguana iguana*. Side view of Hyoid.



extremities. The left is 23.2 mm. long and its companion slightly shorter.

**Hyoid, Side View:** In the usual or dorsal view of a lizard hyoid the tips of the ceratohyals and the first ceratobranchials often cross one another, and the second ceratobranchials appear to extend straight back between the other elements on the same plane. To reorient this optical illusion of a flat plane point of view I have had the lateral view of the iguana's hyoid drawn. Text-fig. 5.

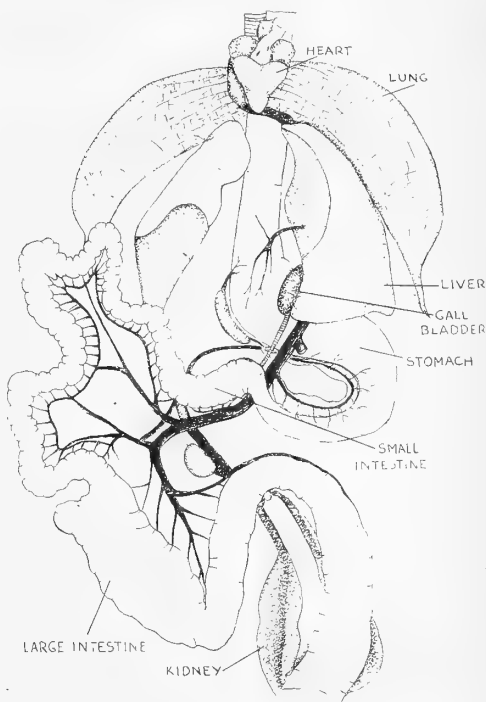
Here we have in dotted outline the toothed upper jaw, and a corresponding outline of the scale-denticulated dewlap or gular wattle. The glossohyal is seen to project forward in support of the tongue, the ceratohyals and first ceratobranchials curve up and around toward their former connection with the auditory meatus. The downward and backward directed second ceratobranchials play an important part in supporting the great throat dewlap. It is difficult, however, to understand how they can play an efficient part in the extension of the wattle, without simultaneously elevating the tongue. The apparent strong ossification suggested by the scarlet dye of the KOH is very evidently completely subordinate to the elasticity of the cartilage foundation.

**Food:** Two iguanas shot on March 24, 1919, 450 and 640 mm. in length, had the crops crammed with hundreds of small, unchewed leaves, packed tightly together like the leaves of a book, each leaf being about a half-inch across. The stomach was equally filled with the same material crushed and comminuted into a greenish pulp. Leaves and petals of flowers seem to be their chief diet, but they will eat pawpaws, jungle cherries and wild guava.

**Enemies:** On January 4, 1921, a small iguana, less than 300 mm. over all, was dropped almost at my feet by a swallow-tailed kite, *Elanoides forficatus yetapa*, as it swooped across the trail east of the Kartabo

laboratory. We have seen a jaguar in full pursuit of a large iguana.

**Breeding:** On September 26, 1922, four eggs were found buried under a bank, partly washed out by the rains. They corresponded exactly with ripe eggs taken from a female iguana. These eggs were one-third developed and showed an interesting disparity in shape and weight. One was round, the others elongated ovals. The shell was chalky white where not stained, rough, minutely and irregularly pitted. The size varied from 42 and 46 to 47.3 and 50.8, with an average of 44.5 by 49.4 mm. The weight extremes were 44.4 and 75.8, averaging 58.3 grams.



TEXT-FIG. 6. *Iguana iguana*. Gross anatomy.

Seven eggs were unearthed by a pet monkey at the foot of a dead stump on October 3, 1920. One egg was a small, round, runt, the rest were straight-sided ovals.

*Habits:* On February 24, 1942, five days after our arrival at Carpito, Venezuela, I noticed that a tall bare tree at the western edge of our compound had a single clump of buds looking like a small parasitic plant high up among the naked branches. We later learned that this tree, a relic of the cut jungle, was eighty-six feet high, and was a Yellow Puoi, *Tecoma serratifolia*. On March 3 the tree showed 17 widely scattered panicles of golden yellow bloom, besides scores of opening buds. On the eighth of the month I saw a four-foot iguana high up among the scanty flowers. From 6:30 A.M. to 1:30 P.M., at least, he remained motionless. The next day the lizard was in the same crotch at 7 in the morning and as far as I know had not moved at 5:45 P.M.

From March 11 on, the iguana was a permanent resident of the tree. An account of his activities on this one day will suffice for all others. He seemed to slumber soundly during the morning, although with my 40-power binoculars I could see his eyelids move now and then. At 11 o'clock he began to climb slowly up and about, and at 1 P.M. he was in the midst of the very topmost cluster of bloom, eating all he could reach and he could reach any he chose. His long tail hung down and he sometimes slipped on the slender bending twigs, and hung on with only the toes of one fore limb. The toes of all four have the power of locking tight about twigs which bend far down with his weight. At first he selected the full-blown flowers but later began on the buds. When sprawled out at the very apex of the tree, one hind leg would occasionally hang loosely, the other clinging with only the middle toe, as he edged slowly out toward the outermost flowers, although four or five other clusters were much nearer on stronger branches. He seemed to enjoy taking chances, and he never gave up. If a first attempt to reach a certain blossom failed, there followed another and another stretching of his neck, then out went his tongue, although it protruded hardly at all beyond his lips. At last he crept an inch nearer, the whole branch bending slowly far over, and when almost upside down he licked in the bud and swallowed it without chewing. On turning to descend he slipped twice and both times hung reversed by his hind toes alone. When he was able to keep his position by means of three feet, the toes of the fourth were used to hook and pull the twigs or panicle to his mouth. The tree was 150 feet from the laboratory porch and 86 feet high, yet the 20 or the 40 diameter binoculars showed every wrinkle of his scaly skin,

every tiny fly that alighted on the edge of his eyes.

On March 19, I noted that the iguana was back after three days' absence. In mid-morning he climbed up the tall bare trunk, and on to the very topmost branch and as all the blossoms were gone he devoured a precocious, long, slender, bean pod, the only one on the tree. It hung vertically over his head from the slenderest of twigs and his lips barely touched the end of it. The wind was blowing and as it swung back and forth he snapped at it and now and then bit off a short section. He never was able to secure more than a fraction. On April 11, the tenant of the Puoi again returned after a week's absence, spending the morning climbing about, plucking and eating the last blossoms of the season, even taking the small, green leaf buds as well. Again he showed his ability to cling by hanging with the toes of one hind foot, both fore feet engaged in pulling a branch toward him, while the other foot dangled in mid-air. On July 10, I noticed the great lizard asleep in a crotch among a mass of new green leaves, and I saw him for the last time on July 24. In the night of July 26, the great tree blew down and the iguana vanished forever.

*Plica plica* (Linnaeus, 1758).

(Plate III; Fig. 9).

*Names:* Spiny Tree Lizard. Agama (Creole). Ing-wallack (Akawai Indian).

*Range:* Northern South America.

*General Account:* A medium-sized, arboreal, insect-eating lizard. Found occasionally on rocks along the river, usually on bark of jungle trees. General characters, broad head and body, slight spiny crest on back and several spiny tufts on neck. Dark green above with wide dark bands mottled on body and solid on limbs and tail. Chin whitish, throat black and necklace black. Sides of head and under parts orange when in full color.

Male adult, No. 68, Kartabo, July 23, 1920:

*Measurements:* Total length 373 mm., head 10 per cent. of length, body 23, tail 66, fore leg 20, hind leg 30 per cent.

*Color in Life:* No. 68; Head yellowish-olive, deeper toward snout; back deep grape green, with seven wide mottled bands of black, the anterior one a collar, the posterior on the tail just back of the hind legs. The upper arms and legs similar in color and pattern, there being three mottled cross bands on the arm and four on the leg. On the lower part of the limbs, digits and tail, the bands become solid black and the green gradually pales to olive gray. There are six bands from elbow to tip of toes, eight from the knee down, and thirteen on the tail.

The black, mottled nuchal collar is mixed



TEXT-FIG. 7. *Plica plica*. Position on tree.

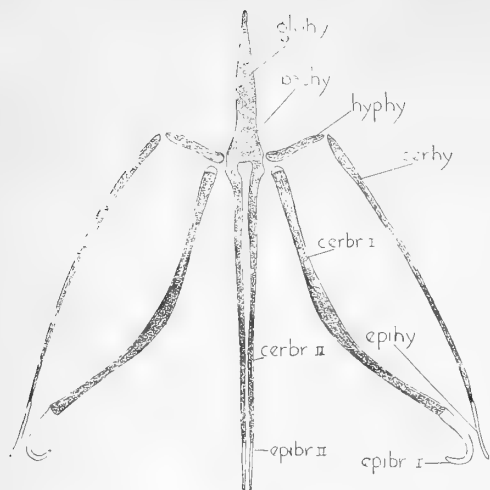
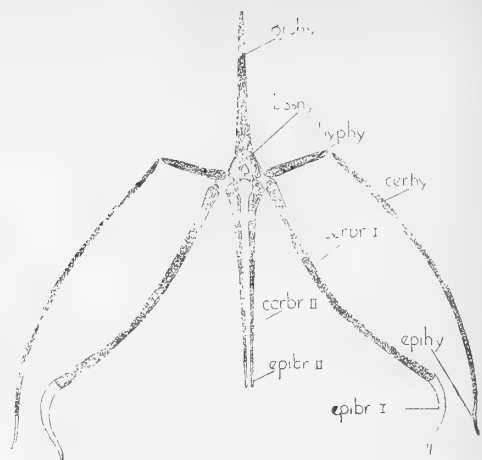
with smoke gray and changes abruptly on the side neck to black, which broadens out on the throat. Anteriorly this fades gradually through light olive gray to cartridge buff on the chin. Ventral surface: black throat narrowly bordered posteriorly with citron yellow, shading into apricot orange which covers the entire under body, thighs and ventral tail, paling to yellowish-white on distal limbs, soles and tip of tail.

Eyelid light grayish-vinaceous; pupil almost round with slight irregularity at bottom. Iris maize yellow, densely flecked with orange and gray, and a narrow inner ring of gold.

*Arboreal Adaptations:* Almost every scale has a sharp protruding spine and a sharp keel. Rubbed the wrong way on its soles, thighs, belly, chin or under tail it feels like

razor grass, and these projections must be of great help in sustaining its position on bark. The fingers are very long and the claws exceedingly long, sharp and bent downward. The exposed dorsal and throat patterns are highly protective, mottled dark and green. In its usual position, upside-down on trunk, the throat patch becomes a shadow and the head an irregular branch stub. The orange of head and sides are of slight conspicuousness.

A female about a foot in length was discovered by accident about 12 feet up on the trunk of a smooth-barked tree. She was in a most remarkable attitude, raised high so that no shadow was cast. I went on down the trail and two hours later, when I returned, the lizard had not moved a muscle. As seen from the sketch made on the spot

TEXT-FIG. 8. *Plica plica*. Hyoid of adult.TEXT-FIG. 9. *Plica plica*. Hyoid of newly-hatched lizard.

by my artist, it was head downward, with practically the entire weight supported by one hind leg, which, attached by two or three claws, was stretched out at full length. One front leg extended straight downward, and the other curved slightly upward. The dorsal crest and spiny neck tufts broke up the outline, while the mottled green color above made it the same color as the bark. It was by the merest chance that I discovered it. Text-fig. 7.

*Hyoid*: Coll. No. 3549, Kartabo, June 30, 1924, adult male, total length 325 mm. Text-fig. 8. Glossohyal rather short, relatively wide, like a narrow tongue in shape, 7 mm. in length. The mid section is very slightly wider than where it merges into the basi-hyals. These elements show very little lateral thickening, and only a slight, shallow concavity indicative of a lateral socket. From the upper part of this area arise the hypohyals, short, slender, 3.5 mm. in length, directed slightly forward. From their tips, with no evidence of specialized juncture, spring the long, very slender ceratohyals, 16.5 mm. in length, at a backward angle of 50 degrees. Transparent, short epihyals terminate these elements.

Below the origin of the hypohyals arise the stout, first ceratobranchials, with a flattened, proximal cartilaginous cap. In dorsal view, these bones bend sharply outward for a distance of 17 mm., terminating in curved, hyaline, first epibranchials. The arms of the basihyals are continued posteriorly by the long, slender second ceratobranchials. Proximally these bend inward toward each other, and maintain a closely parallel but quite separate course for their entire 15 mm. Typical short second epibranchials are at the extreme ends.

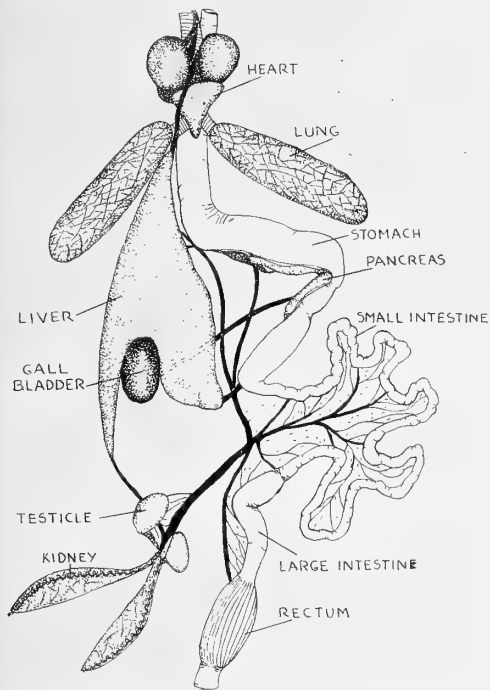
A young (24 hours old) *Plica plica*, Coll.

No. 870, Kartabo, April 25, 1919, total length 185 mm., shows distinct differences from the hyoid of the adult. Text-fig. 9. The relative lengths of the glosso- and hypohyals are the same, but there is relatively much less of antero-posterior development in the three elongated elements of the hyoid complex. The ceratohyals and first ceratobranchials in the young lizard present no change in their respective relative lengths, but the second ceratobranchials, instead of extending posteriorly an appreciable distance beyond the others, are hardly more than three-fourths of their length. This delayed ontogenetic development of an exceedingly primitive character, whose secondary function will be to assist in the operation of the very specialized wattle or dewlap, is significant and interesting.

The only other noticeable character peculiar to the juvenile lizard is a distinct thinning, almost a perforation, in the center of the basihyal mass or the base of the glossohyal. There is also a decided constriction of the proximal attachment of the second ceratobranchials into a neck. We can easily imagine that at a slightly earlier stage these elements would be pinched off altogether, thus isolating them and approximating a still more primitive condition.

*Gross Anatomy*: Adult male, Coll. No. 68, Kartabo, July 23, 1920, total length 373 mm. Text-fig. 10. The stomach is elongated, with the short, narrow duodenum turned right at an acute angle. The pancreas is narrow but long, extending along the duodenum and half way up the side of the stomach, partly overlying the long and narrow spleen. The small intestine is narrow and much convoluted, the folding recalling that of a young alligator. The cloaca is large and volum-

inous. The liver is shaped like an isosceles triangle. It is large and long, covering most of the intestines. It is deeply incised around the gall bladder, with a deep groove extending anteriorly for some distance. Measurements are as follows: small intestine 145 mm., large intestine 23.5, cloaca 23.5, duodenum 15, spleen 9, liver 48 mm., liver weight 1.1 gram. Weight of lizard, 76.7 grams.



TEXT-FIG. 10. *Plica plica*. Gross anatomy.

**Food:** The contents of six stomachs were (1) five beetle grubs; (2) large millipede, cicada, many red and black ants; (3) solid mass of more than 100 ants; (4) 85 termites, few winged ants, small scorpion; (5) large black bee; (6) bee, 40 *Atta* ants, several beetles, large roach and a spider.

In captivity these lizards accepted almost any kind of insect, including butterflies and moths of many species. With my large binoculars I was watching a *Plica* thirty feet up a tree when a cicada which attempted to alight on the lizard was seized like a flash and eaten. In Caripito I saw three of these lizards high up in tall jungle trees, all of them on the bark, and all quietly waiting upsidedown.

**Breeding:** A female taken May 13, 1924, contained two eggs, soft, but well developed, and soon to be laid. On May 24 of the same year a male was shot in full breeding condition.

***Plica umbra* (Linnaeus, 1758).**

(Plate III, Fig. 10. Plate V, Fig. 14).

**Name:** Smooth-necked Tree Lizard.

**Range:** Northern South America.

**General Account:** At a distance, the chief difference between adults of *plica* and *umbra* is the black dewlap and, when closer, the presence of the spiny neck tufts in the former. *P. umbra* lacks both of these. In habitat, usual position on tree trunks, general reactions, and diet, the two species are indistinguishable. The head is short and broad, eye ridge prominent, color above in general olive with darker bands and mottlings; greenish-white or yellowish below. If we concede the power of concealment is equal and the chances of discovery the same, then *umbra* is about three times as abundant, judging by the number seen or collected. The relative number of young individuals observed is very much greater in *umbra* than in the other species.

Male adult, No. 14, Kartabo, April 23, 1919:

**Measurements:** Total length 256 mm., head 7 per cent. in length, body 24, tail 69, fore leg 16, hind leg 24 per cent. Weight 12.2 grams. The weights of male lizards varied from 10 grams for a 203 mm., specimen to 22.5 grams for one of 300 mm.

**Color in Life:** The principal pattern and color variations are covered by the following four descriptions.

**Specimen No. 14, male:** Upper surfaces and sides generally pea-green, becoming more yellow and changing to light yellow drab on the tail. Everywhere irregularly blotched with black, the black spots coalescing more and more as they approach the hind limbs, and finally on the tail becoming large spots of sepia. Upper arms and legs irregularly spotted with blackish-brown, much more concentrated on the tibia and fore arms, forming bars. At the articulations of the fingers and toes a spot of sepia. Upper and lower labials, head below a line from the nostrils over the canthus and eye to the tympanum, irregularly spotted and mottled with various shades of green, light greenish-yellow predominating. Lower surface of head, body, arms and legs pale pinkish-buff, changing to apricot yellow on tail. A decided orange cast between the two longitudinal folds of the gular region.

**Specimen No. 14a, male breeding, July 27, 1920, total length 284 mm.:** General color of back absinthe-green becoming more intense on shoulders and dull lime green on limbs and tail. Scales of head and face a mixture of brilliant and pale grenadine pink, mottled with gray and green. Pineal scale lime green with gray central dot. Small dusky spot on back of neck. Five backward-pointing, transverse dorsal bands, the first deep black with central portion of dragon's



TEXT-FIG. 11. *Polychrus marmoratus*. Posture in tree.

blood red, connected laterally with the second which shows less intense black and more red. Last three bands paler red, with black framing before and behind, the sides of the bands breaking more and more into various sized black spots. Beginning at the thighs, 17 dull black bands extend to tip of tail, the bands being twice the width of the interspaces. Limbs and feet banded like the tail.

Specimen No. 808, male breeding, September 29, 1922, total length 300 mm.: Above, head blue green, body and limbs pale jade green. Broad, black irregular bandings, six across body, two on upper and two on lower arms and legs, and 15 on tail. The color on the tail changes gradually to citrine brown. Below head and jaws tea green, shading centrally into old gold; body and limbs smoke gray. An unusual character is four marks of strong yellow ochre around vent, forming three, narrow, tall triangles pointing forward along abdomen and outward along thighs; and a central spot directly in front of the vent. The dewlap, usually hidden, is lemon yellow.

Specimen No. 2661, female, March 24, 1924, total length 280 mm.: Top of head and neck gray. A short crest of cream and black pointed scales running from above tympanum to mid-body. Face and all labials bluish-

glaucous with patches of straw yellow in front of typanum each side of eye. Side of neck straw yellow, clouded with gray. Gular pouch light ochraceous buff becoming darker on chin and with a patch of red between humeral and gular folds. A broad band of black obliquely across shoulder. Upper body and limbs forest green with eight transverse bands of mottled brown and black, others on upper limbs. Body color changes to red brown on tail, brown at tip, which has nine mottled spots of black. General ventral color vinaceous fawn, deeper around vent and brown under tail. Iris dark speckled golden, with clear inner pupil ring.

**Food:** Four stomach contents were as follows: (1) 8 beetles, 2 ants, 1 katydid; (2) 27 large black ants, 3 small beetles, 4 small centipedes; (3) numerous black ants and beetles, 6 centipedes; (4) 2 June beetles, 30 small black ants.

**Breeding:** A male and female lizard (No. 191a) were taken while mating on September 9, 1919. Other lizards in full breeding condition were collected in April (3 records), May (3) and October (2). Surprisingly small lizards, less than 220 mm., both male and female, were found to be breeding.

A female, No. 216, October 14, 1920, kept in captivity for several weeks, laid two oblong eggs, 10 by 20 mm., white, with



TEXT-FIG. 12. *Polychrus marmoratus*. Posture in tree.

equally rounded ends, the surface rough, with many irregularities tending in a transverse direction.

*Courtship*: Several times we saw the violent bobbing of the head, the lizard standing upsidedown on a trunk, stretched high on its fore legs, always in the presence of another individual. In the case of the pair shot while mating, both sexes bobbed when first observed. This mated pair were distinguished by the following characters: Male, total length 290 mm., weight 17.7 grams. In general mottled dark green above, with dark bluish head, and much yellow buff about the vent and thighs. Female, total length 246 mm., weight 15.7 grams. Dull olive green above with greenish head and no yellow buff. All dorsal colors subdued and so merged that no specific description is possible; exactly like the mottled, lichened tree trunk to which she clung.

***Polychrus marmoratus marmoratus***  
(Linnaeus, 1758).

(Plate IV, Figs. 11-13.

Plate V, Figs. 15 and 16).

*Names*: Many-colored Tree Lizard; Marbled Lizard. Gamma or Colonial Chameleon (Guiana Creole). Ee-wang-quee-buh-nah (Akawai Indian meaning, "Hungry father").

*Range*: Northeastern South America.

*Occurrence*: Both at Kartabo and Caripito this species is fairly common and probably might be called abundant if our eyes were keen enough to detect more than a small percentage of those clinging motionless and simulating their backgrounds on the branches of bushes and moderately tall trees.

*Color in Life, General*: This lizard defies any exact description as to pattern or color. The most usual appearance is of a large,



slender, green saurian with two jet black lines radiating back from the eye, one over the ear, and one to the gape. Usually there is a wide whitish band along the side and a brownish cast to the tail. The entire lizard can become wholly green or altogether brown, and often the back develops a series of five or six broad, oblique, straw yellow bands separated by darker bands. The under parts may be immaculate white, or mottled and marbled with green or brown.

The markings of the dewlap are varied, often being very obscure, or occasionally flaring as several longitudinal scarlet slashes. The iris shares in this variability. Of three full-grown lizards one had the eye golden-brown marked with silver; a second deep wine color with inner ring of gold, and a third showed the upper quarter warm buff and the rest tawny.

The males are smaller than the females, the average total lengths of nine males being 385 mm. and of 13 females 478 mm. Part of this extra length is taken up by extra body length in the females, as the tails of the males average 72 per cent. of the total length as compared with 68 per cent. in the females. The largest female I have measured was 506 mm.

The weights varied considerably, being greater of course in breeding females. Extremes in adults of both sexes were 18.6 and 36 grams.

The femoral pores varied from nine to fourteen, sometimes in the same individual. Of 12 males, two were symmetrical, in one the left leg had the larger number while in the remaining 10 there were more femoral pores on the right than on the left thigh.

*Color in Life:* No. 637, Kartabo, May 14, 1919, total length 330 mm., although small was fully adult. It permitted a close approach and was colored as follows: lumiere green on head, sides and under parts of the body, darkening to forest green on the dorsal surface of back and limbs. Labials, chin and throat pale lumiere green. A few irregular and indistinct cephalic, dorsal and femoral spots of vinaceous brown, and the entire tail, beginning abruptly at the vent, of this color, with about sixteen nodes of lighter bands bordered with darker. A broad irregular band opalescent white from shoulder back along sides, breaking into irregular spots on the outer border of femur and ulna. The most conspicuous marks are the two lateral head lines of black which I have mentioned. A third almost as distinct extends directly downward across the upper and lower lips, while four other broken ones radiate upward to the supraoculars, each ending in a distinct black spot.

No. 185, female, August 16, 1920, 452 mm. in length, was of a general vinaceous brown over all the dorsal parts, and fawn

color below. This color held after death. Another female was also brown in general with the dorsal oblique bands well developed. This pattern also held after death and in the flat mounted skin, twenty-five years after capture, the pattern and colors are distinct as ever.

*Change of Color:* September 14, 1917, caught a male *Polychrus* 432 mm. in length. It was green in general but after five minutes in a vivarium it turned almost uniform clove brown above, with abdomen and broad tail bands light pinkish wood brown. Faint traces of green remained around the eye and ear, and a large round patch on the left side, just in front of the insertion of the fore leg, remained brilliant green. The change to this sombre color occurred within thirty seconds. After fifteen minutes the green color began to reappear. One week later when put in preservative, the green color returned in full strength, turning at once to an abnormal blue.

*Habits:* *Polychrus*, more than any other lizard I know, depends on two factors of safety, change of color to approximate the immediate surroundings, and most remarkable strained and posed attitudes which are maintained for considerable lengths of time.

An example is specimen No. 637 caught on a low branch on the edge of the jungle near the Kartabo laboratory. It was hugging the end of a brown branch which was covered with a mottling of lichens of almost the same color and pattern as its body. Its tail hung loosely outward exactly like a side twig of the branch, and as I approached it only gripped more tightly. At last it raised itself on its fore legs, distended its dewlap as wide as possible, and then rushed through a tuft of leaves for a few inches, and again clutched the branch, allowing the right fore leg and the left hind leg to dangle free. It now changed to a dominant green and before my eyes melted into its new environment, wholly unlike the brown previous color. I seized it with a sudden, swift motion, when it opened its mouth and did its best to bite me. A moment later it succeeded and the sharp teeth and jaw muscles gave force enough to make several deep tears in the skin. The claws of this lizard are long, sharp and curved and exceedingly uncomfortable when tightly gripping one's hand.

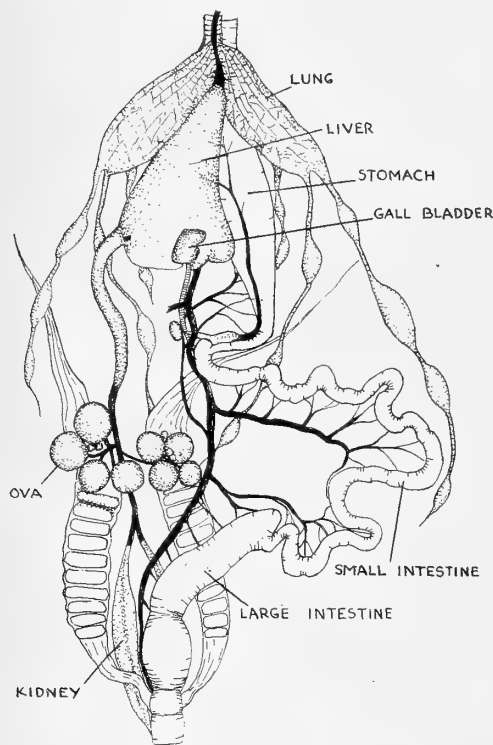
Several times when by accident we spied one of these lizards near the laboratory I took the artist out and had a sketch made direct from the position. In one case the lizard kept the pose for more than three hours, although it looked most strained and uncomfortable. Two of these may be seen in Text-figures 11 and 12. In the first, the lizard is twisted around a small branch,





dence of hypobranchials. The ceratobranchials curve gradually outward and are slender, narrow rods, ending in a moderate, curved, hyaline, pointed tip of epibranchial derivation, which curves around in close proximity to the tips of the hyoid arch.

The second ceratobranchials are extremely elongated, parallel and very close together, being surrounded by a hyaline envelope, and joined together by a delicate membrane. The tips end in a transparent spatulate enlargement. Proximally, no distinction is visible between the ends of the basihyals and the beginnings of these second ceratobranchials. *Measurements*: Lingual core length 7.7 mm., visible glossohyal rod 4.8, hypohyals 3, ceratohyals 13.7, first ceratobranchials 15.4, second ceratobranchials 18.6 mm.



TEXT-FIG. 14. *Polychrus marmoratus*. Gross anatomy.

*Gross Anatomy*: No. 185, Kartabo, female, August 16, 1920, length 452 mm., nostril to anus 124 mm., weight 37 grams. Small intestine 117 mm., rectum 23, cloaca 16 mm., liver weight .8 gram. Text-fig. 14. The body walls of the abdomen are lined with a blackish membrane. Each lung sends down three long, narrow, noded tentacles which may be inflated, and which pass between the folds of the intestine, around the

ovaries and down to the kidneys. The lower portion of the stomach is curved to the right. Each ovary contains four large eggs with yolk almost of full size. There are a few very small ova.

The large epigastric vein enters the larger portal vein some distance below the liver; the mesenteric enters it more posteriorly, as does the splenic. The portal passes over the pancreas and under the duodenum, being attached to the walls of the intestine, after the mesenteric has entered it. Arising from the cloaca, it passes forward to meet the mesenteric, being joined by branches from the rectum and a large vein from the lower portion of the small intestine. A system of veins drains from the stomach into the splenic and thence into the portal. Several gastric veins run directly into the left lobe of the liver from the stomach. The spleen is small and bean-shaped.

*Tropidurus torquatus hispidus* (Spix, 1825).

(Plate VI, Fig. 19).

*Name*: Spotted Tree Lizard.

*Range*: Northern South America.

*General Account*: A rare lizard at Kartabo and not recorded from Caripito. Only four specimens taken of which two are lost. At a distance probably confused with young *Plica*.

*Measurements*: Adult male, No. 306, April 25, 1919, length 175 mm., head 8 per cent. of length, body 24, tail 68, fore leg 16, hind leg 25 per cent.

Juvenile male, No. 2768, April 21, 1924, Color Plate 706, length 127 mm., head 8.6 per cent. of length, body 28, tail 63.4 per cent.

*Color in Life*: No. 306, olive brown above marked with black. Anteriorly these markings are in the form of vertical bands, three passing through the eyelids, followed by eleven from the nape to the mid-back. When the fore limb is adpressed to the body the 5, 6, 7 and 8th bands are continued across the upper arm. The posterior back and the tail are unmarked. Under parts from chin to vent bright salmon. Sides of chin and throat marked with broken lines, with a very heavy converging broken band on the mid-throat and side fore shoulder. Two transverse broken bands extend across the ventral fore body, and the lower sides of the body are rather finely spotted.

The dorsal crest is well marked, starting on the nape and ending abruptly half way down the tail, although this member is not regenerated. The crest is low and even, as far as the sacral region where it doubles its height and maintains this to the posterior end.

In the juvenile specimen, No. 2768, the

upper surface is bluish-gray, the occipital plate black, with a wide, conspicuous backward-pointing V of creamy white. Dorsal crest with wide spaced bands of black. Four narrow black lines radiate from the eyelids, forward, down and back. Five additional, oblique broken black bands are visible between the nape and shoulder, the posterior one a strong, solid streak in front of the insertion of the fore arm.

Adult female breeding, No. 306a, length 141 mm., is dark above, paler below, spotted and mottled coarsely on chin and throat, back to mid-body.

**Breeding:** Specimen No. 306a contained two eggs about to be laid, apparently full-sized, measuring 10 by 15 mm., one on each side of the body.

***Uranoscodon superciliosa* (Linnaeus, 1758).**

(Plate VI, Figs. 17 and 18).

**Name:** Gray, or Brown Tree Lizard. Agama (Creole). Yamu-koo-roo (Akawai Indian, "crossing over water, because he swims creeks and makes bubbling noises when swimming").

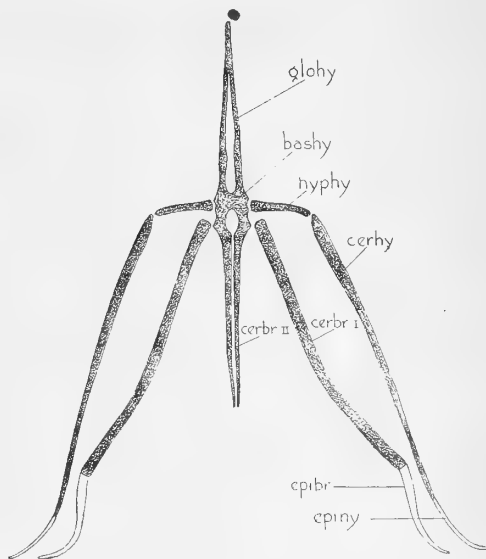
**Range:** Northeastern South America.

**General Account:** These lizards are not uncommon, both at Kartabo and Caripito, but are doubtless more often overlooked than discovered. They are among the dullest of monochrome saurians with habits directly correlated with their pigmentation. They live chiefly in dense jungle, but are also found on rank growths along the shores of creeks and rivers. Most of the day is spent in clinging close to a twig or branch as brown as they are, and only by accident did we ever locate them. They never try to escape, but allow themselves to be picked off, legs dangling in mid-air, eyes half open, making no effort to escape or bite. They may be hung on a sleeve and carried back to the laboratory with no concern about their moving. I have put one on a branch in a vivarium and had it remain without movement for 38 hours, although the eyes were open, and the lizard seemed fully conscious of what went on around him. When the gray lizard does move it is with a headlong rush. On level ground I have seen them more than once work up to bipedal locomotion for a few yards. They are gentle and never make any attempt to bite.

**Measurements:** In lizards of 226 to 400 mm. total length, the measurements show little variation. The average is, head 7 per cent. in length, body 23, and tail 70 per cent. Weights, length 150 mm. (3.4 grams), 226 (10), 320 mm. (20 grams).

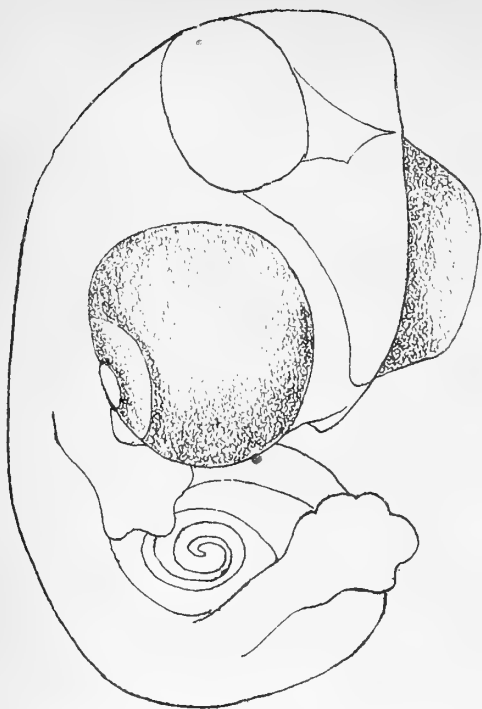
**Color in Life:** Male, No. 810, Kartabo, length 400 mm., September 30, 1922: General color above grayish-brown mottled faintly with spots of buff which are scat-

tered along the side of the head and dorsal crest, and in six large, irregular groupings along the side of the body. Inner edge of eyelids, throat and slight dewlap, and an elongated patch of mottling along ventral surface colonial buffy yellow. Limbs strongly banded with darker color. Whitish-brown below. Iris orange rufous flecked with gold and darker on outer edge. Narrow inner iris rim yellow. In very young lizards there are several pale buffy white lines radiating downward and forward from the eyes across the snout and jaws. A broad whitish band begins back of the eyes and curves over the shoulder and widens into a festooned band along the sides of the body and tail, edged above with black freckling.



TEXT-FIG. 15. *Uranoscodon superciliosa*. Hyoid.

**Hyoid:** Coll. No. 3006, Kartabo, August 19, 1922, total length 240 mm. Text-fig. 15. The glossohyal is 5 mm. in length, wide at the base and gradually narrowing to the anterior tip. The basal two-thirds of its length is perforated by a longitudinal aperture, so wide that the lateral osseous boundaries are as narrow as the beginning of the solid distal third. The basihyals show little lateral thickening, but present two distinct although shallow sockets on the external lateral aspect. From the upper one arise the hypohyals, fairly heavy, 2 mm. long and extending at right angles to their point of origin. Equally slender ceratohyals arise from their tips, and extend obliquely backward for a distance of 9.5 mm., giving rise, in turn, to long, slender epihyals. The first ceratobranchials originate at the lower socket of the basihyals, and are considerably heavier than the ceratohyals, and 8.2 mm.



TEXT-FIG. 16. *Uranoscodon superciliosa*.  
Embryo.

in length. The terminal first epibranchials are longer and thicker than the epihyals. The central foramen in the body of the basi-hyals is a good-sized oval, and the lateral arms are continuous and fused with the posteriorly directed second ceratobranchials, which extend straight backward for 5 mm.,

separated from each other by a narrow, clear channel. No signs of second epibranchials are visible.

In the perforation of the glossohyal and the relative shortness of the second ceratobranchials the hyoid of this two-thirds grown *Uranoscodon* bears a striking resemblance to that of a half-grown *Plica plica*.

**Food:** In captivity one gray lizard lived for a month and a half voluntarily without food, although surrounded and in the midst of plenty. There was little evidence of emaciation. When at last the prolonged fast was broken, the lizard readily devoured quantities of orthoptera, caterpillars and grubs, but showed little relish for termites. A young male taken August 19, 1922, had eaten a millipede and three lepidopterous larvae.

**Breeding:** On August 5, 1920, three miles out along the Puruni Trail, Kartabo, Dr. William Morton Wheeler called to me to come and see a large *Uranoscodon* on her nest. She was in a hollow in a half-broken knot-hole of a decayed log, and had deposited 11 eggs. Unlike the usual reaction of this species she was nervous and timid, and at our close approach she rushed out and up the nearest tree trunk. I stunned her with a bullet on the bark beneath her and put her in a snake bag. She was No. 312, August 5, 1920, length 405 mm., weight 26 grams, Color Plate 216.

The hollow bore evidence of considerable scraping, as if enlarged by the lizard. Remains of old bits of shell of the same character as those freshly deposited hinted at a former occupancy. One egg, accidentally broken, was perfectly fresh.

The 10 remaining eggs weighed 24.4



TEXT-FIG. 17. *Urocentron azureum*.  
Drawing of adult.

grams, averaging 2.4 grams. The average size was 13.4 by 24.3 mm. The shape was rather variable, one end slightly smaller than the other, three noticeably wider across the middle, the rest with sides parallel. The shell was leathery, rather soft, roughened, with low striae extending transversely around the shell. The shells were already brownish, stained from contact with the soil, but they washed to a dull white.

Sixteen days later the embryo was well developed, limb pads entire. Text-fig. 16. At 30 days the embryo measured 33.5 mm., with other percentages as follows: head 19 per cent., body 35, tail 46, eye diameter 12, arm bud 10, leg bud 14 per cent. Either from lack of moisture or other cause the eggs failed to hatch.

On August 22, 1922, six eggs of this species were brought in by our Indian hunter, taken from a hollow 12 feet up a tree. The eggs averaged 13.6 by 25 mm., and in weight 2.7 grams.

***Urocentron azureum*** (Linnaeus, 1758).

*Names:* Spine-tailed Lizard. Tali-tali (Akawai Indian).

*Range:* Brazil and the Guianas.

*General Account:* Two specimens were taken at Kartabo, both of which have disappeared. Specimen No. 41 was found by me among some rocks near the shore at Kartabo, on April 28, 1919. It was 100 mm. in length. Color Plate 35. Identification from the color plate seems certain. Text-fig. 17.

A second specimen was brought in by my collector in 1922, and either escaped before being killed or was lost in transit.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- FIG. 1. *Anolis chysolepis*, breeding male, Spec. 2778.  $\times 3$ . Upper parts brown and gray, dewlap scarlet.
- FIG. 2. *Anolis fusco-auratus*.  $\times 2$ . Pale green with gray markings.
- FIG. 3. *Anolis nitens*, Spec. 530.  $\times 2$ . Light brownish-yellow marked with dark brown, dewlap scarlet.
- FIG. 4. *Anolis nitens* (right) and *Anolis chysolepis* (left). Photograph from life. Natural size.

## PLATE II.

- FIG. 5. *Iguana iguana* on branch.  $\times \frac{1}{2}$ .
- FIG. 6. Head of adult *Iguana*. Natural size.

## PLATE III.

- FIG. 7. *Iguana iguana* half-grown, Spec. 2877.  $\times 2$ . Head and dewlap gray, marked with olive green on body and legs; feet green.
- FIG. 8. Seven eggs of *Iguana*.  $\times \frac{1}{3}$ .
- FIG. 9. *Plica plica*, Spec. 2844. Natural size. Face and upper labials orange, dewlap pale brown and black; body pale blue and green marked with black; legs and toes black banded with lemon yellow.
- FIG. 10. *Plica umbra*.  $\times 1\frac{1}{2}$ . Side of face and labials pale blue, top of head gray, dewlap golden yellow, body and legs green marked with black.

## PLATE IV.

- FIG. 11. *Polychrus marmoratus*, Caripito.  $\times \frac{1}{3}$ . Head, body and legs bright green, dotted with gold; belly and tail gray marked with brown.
- FIG. 12. *Polychrus marmoratus*, Caripito. Head, natural size, green marked with black, dewlap green with scarlet streaks.
- FIG. 13. *Polychrus marmoratus*, Spec. 3544 Female.  $\times \frac{1}{2}$ . Flat skin, brown phase, light golden brown marked with dark brown.

## PLATE V.

- FIG. 14. *Plica umbra*.  $\times \frac{1}{2}$ . Female with eggs.
- FIG. 15. *Polychrus marmoratus* in jungle.  $\times \frac{1}{4}$ .
- FIG. 16. *Polychrus marmoratus*. Seven eggs. Natural size.

## PLATE VI.

- FIG. 17. *Uranoscodon superciliosa*, Spec. 515. Half-grown.  $\times 1\frac{1}{2}$ .
- FIG. 18. *Uranoscodon superciliosa*, Spec. 312.  $\times 1\frac{1}{2}$ .
- FIG. 19. *Tropidurus torquatus hispidus*, Spec. 306.  $\times 2$ . Head, body and upper sides of legs olive green, supraocular scales and all under parts bright pink marked with black.

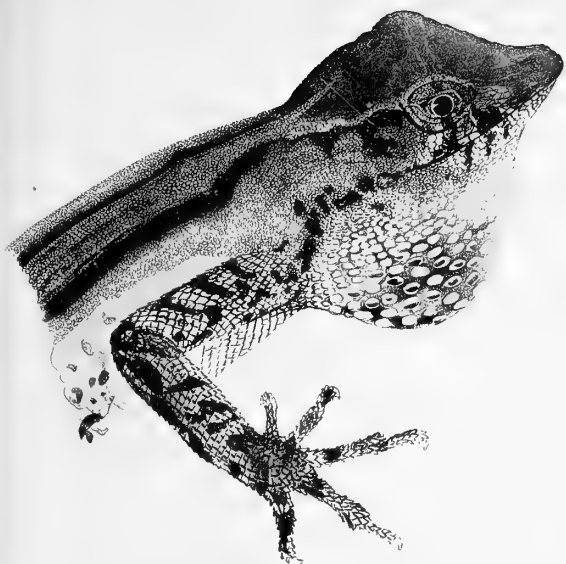


FIG. 1.



FIG. 2.

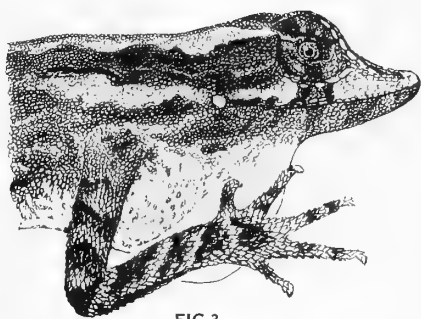


FIG 3.



FIG 4.





FIG. 5.

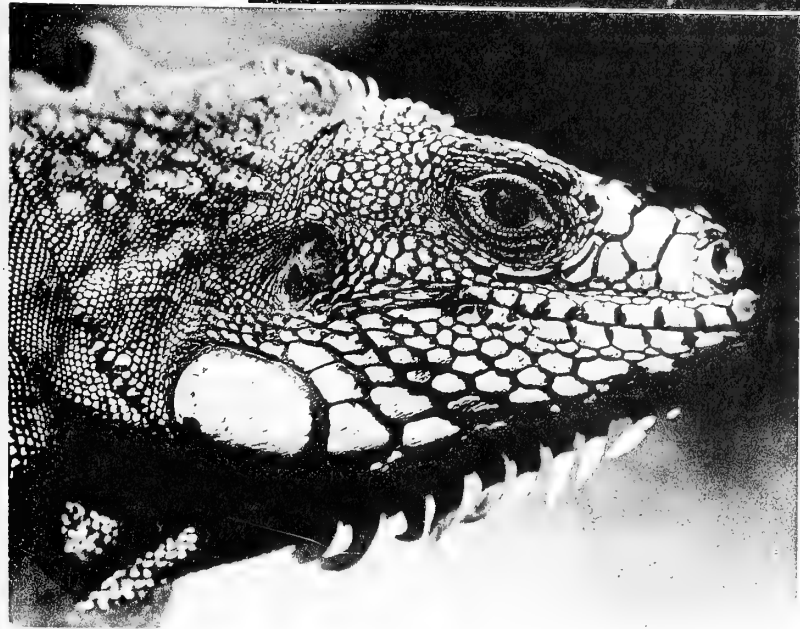
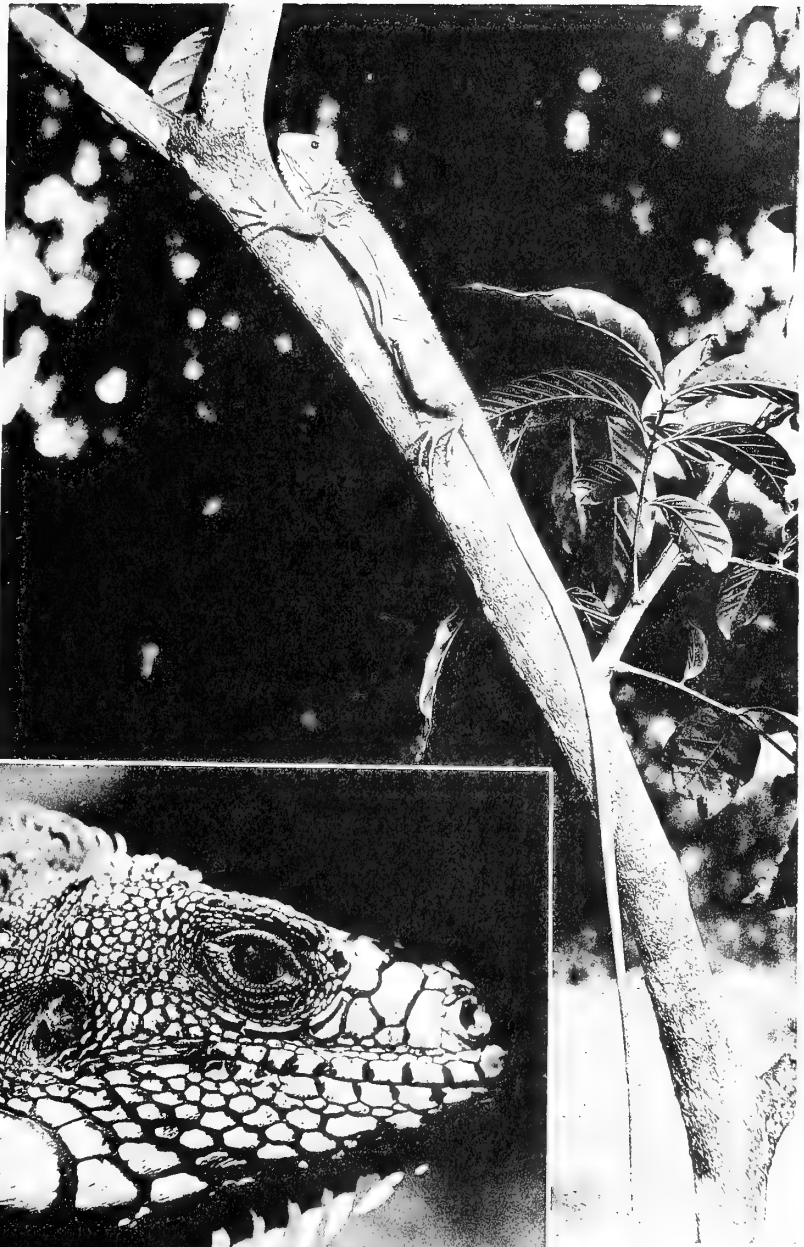


FIG. 6.

FIELD NOTES ON THE LIZARDS OF KARTABO, BRITISH GUIANA, AND CARIPITO, VENEZUELA.





FIG. 9.

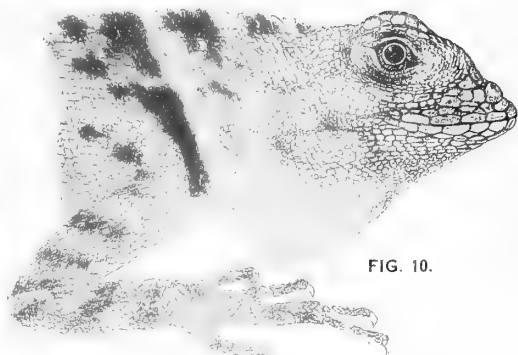


FIG. 10.

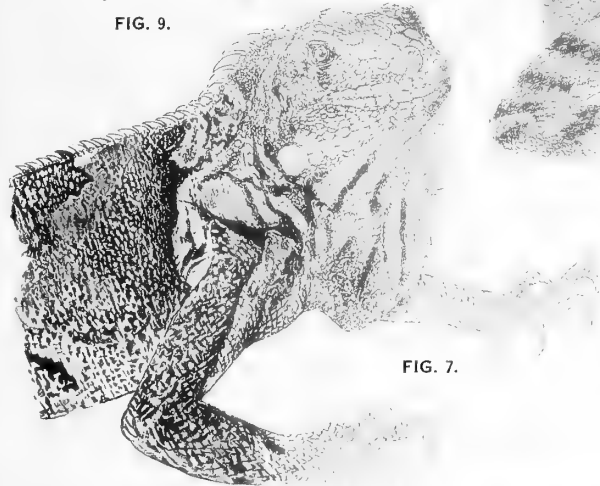


FIG. 7.

FIG. 8.





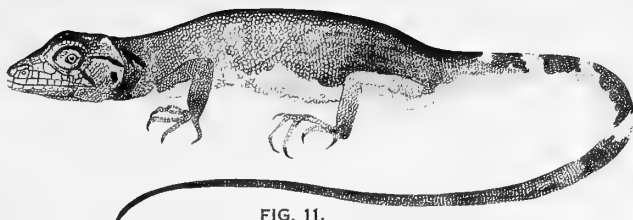


FIG. 11.



FIG. 12.

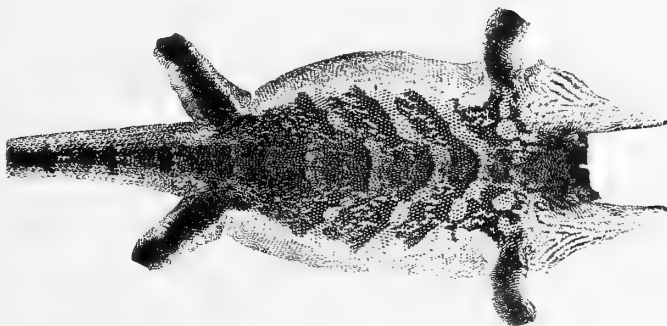


FIG. 13.

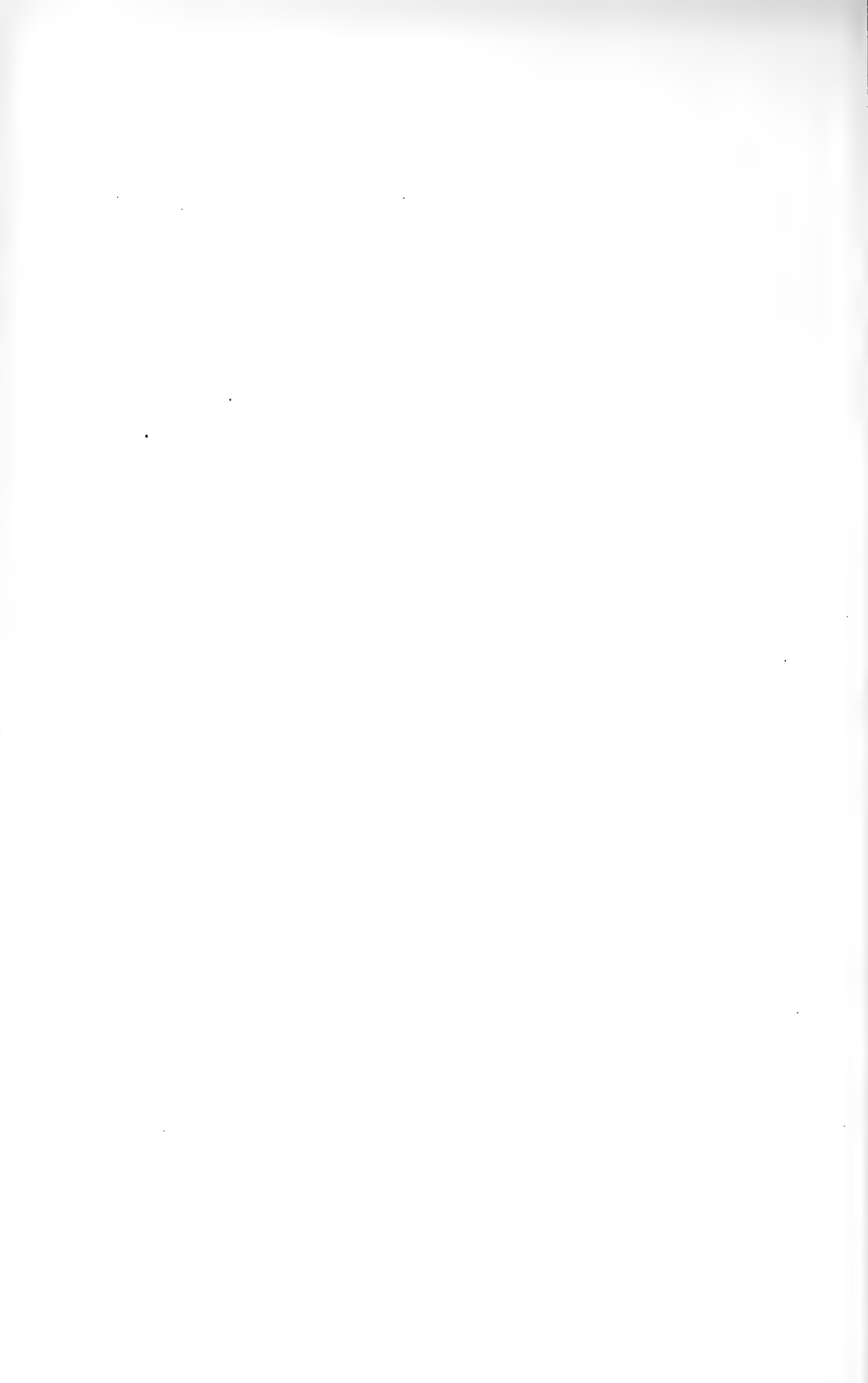




FIG. 14.

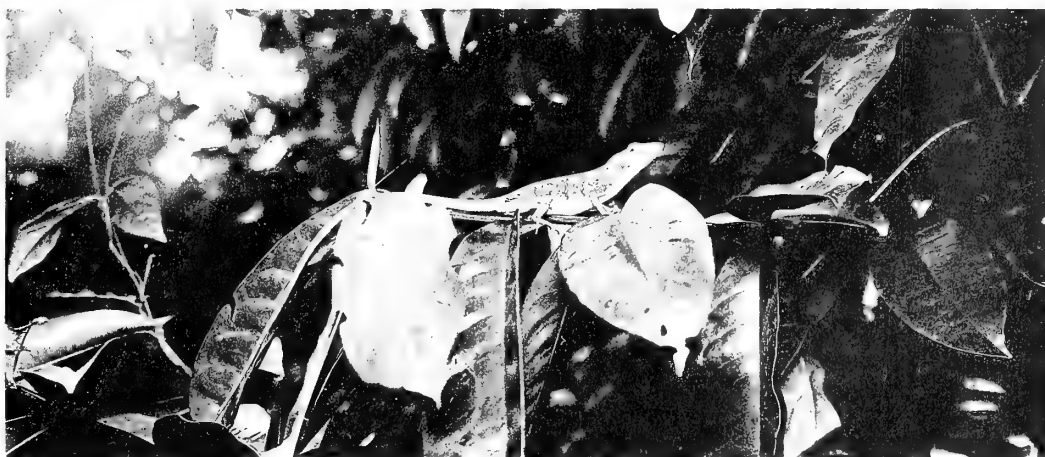


FIG. 15.

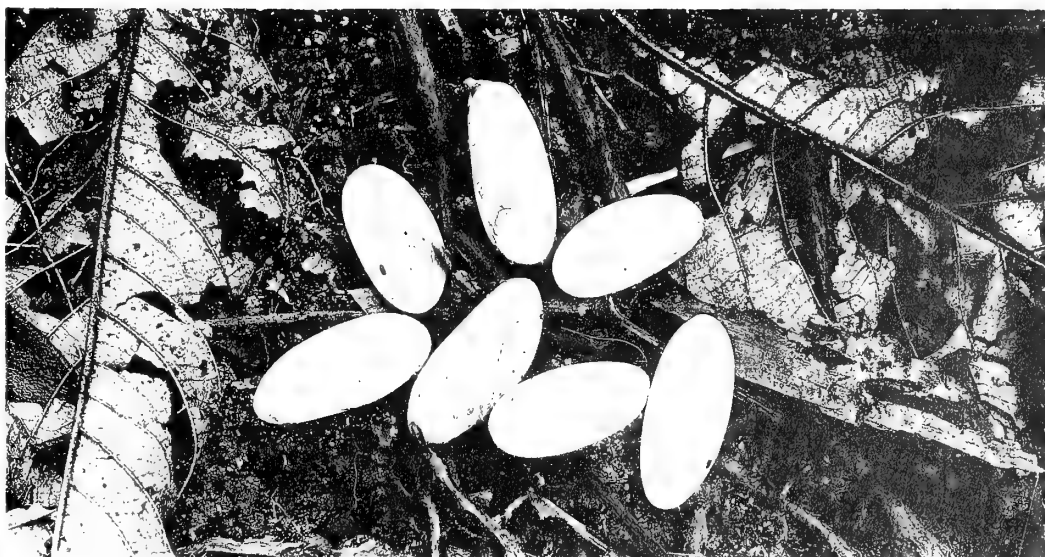


FIG. 16.







FIG. 17.

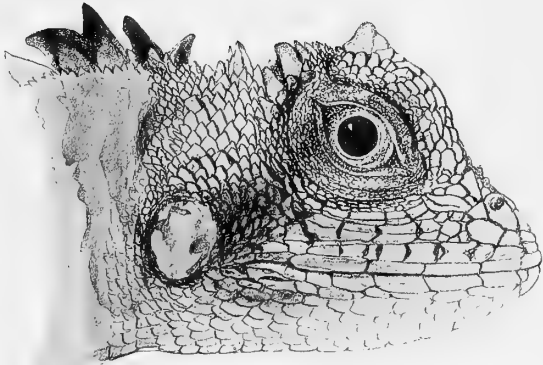


FIG. 18.

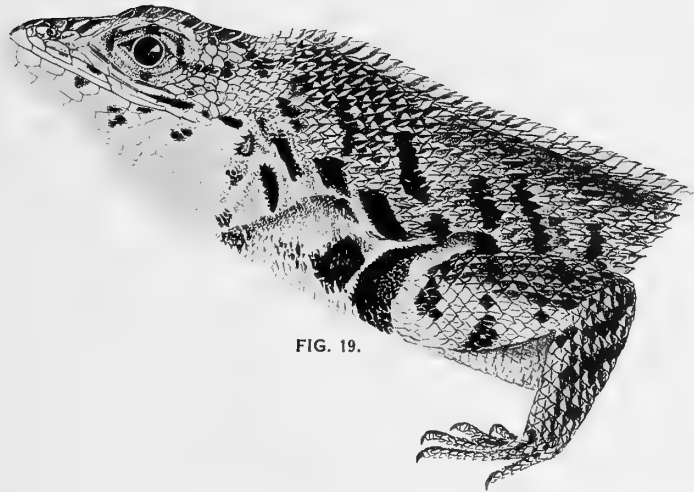


FIG. 19.



## 19.

Materials for the Study of the Life History of *Tarpon atlanticus*.

C. M. BREDER, JR.

*American Museum of Natural History.*

(Text-figures 1-9.)

## INTRODUCTION.

Although the tarpon, *Tarpon atlanticus* (Cuvier and Valenciennes) is a well known sportsman's fish and is sought for sporting purposes throughout most of its range, aside from a considerable sportsman's lore there is surprisingly little known about its life history and habits, in spite of the fact that most of its life is spent in thoroughly accessible places.

An attempt to obtain scientific data on the life history and behavior of the species was initiated in 1938 under the encouragement of the late Mrs. Gracia Rhinehart. For this purpose she gave financial support and provided a location in the heart of tarpon country. To this end a field laboratory was established on Palmetto Key, in Pine Island Sound on the West Coast of Florida, under the aegis of the New York Aquarium. The cooperation of the Peabody Museum of Natural History, made possible through the good will of the Director at that time, Professor A. E. Parr, and the Zoologist, Dr. Stanley Ball, has been invaluable to the work. It took the form, to a large extent, of lending the Museum Collector, Mr. Marshall B. Bishop, for long periods of time. His indefatigable services have been of the greatest value. Among other things, practically the entire burden of the tagging operations devolved on him. The United States Bureau of Fisheries (now part of the Fish and Wildlife Service), through the good offices of Dr. Elmer Higgins and Mr. Robert Nesbit, enabled us to use government tags for the tagging operations, a feature we found of much value. Later Mr. Nesbit was kind enough to undertake to make celluloid imprints of certain of the tarpon scale samples, a matter which greatly facilitated the study of the markings on them. He employed a new method suitable for these large scales which was devised by him and without which we would have been considerably handicapped. Scales of the smaller fish were mounted for study by Mr. Paul Benzer of the National Youth Administration at the laboratories of the

old New York Aquarium. When the laboratory work was about one-half finished, operations were transferred to the American Museum of Natural History where most of the remainder of the work was carried out in the laboratories of the Department of Animal Behavior, through the courtesy of Dr. Frank A. Beach. The manuscript was finished in the Department of Ichthyology.

The field laboratory and its location, about four miles south of Boca Grande Pass and three north of Captiva Pass, was found ideal for the purposes. Both of these places are used to a great extent for tarpon angling. Notwithstanding these advantages, the accumulation of pertinent data was not easy and there is still much to be done, now largely forcibly suspended by the restrictions imposed by war. For this reason, as well as others, it was thought best to make available the data and their analysis so far as we have been able to carry it.

A considerable number of students not already mentioned assisted with many of the items under study. They include the following list, to whom we are grateful: Mr. L. L. Babcock, author of "The Tarpon;" Dr. Richard Cox, New York University; Mr. B. Dontzin, Cornell University; Mr. L. A. Krumholz, University of Michigan; and Mr. Stewart Springer, Shark Industries, Homestead, Florida.

To this list should be added many anglers, local fishermen and others to whom thanks are due, for one item or another. Especial mention must be made of Mrs. Mary Roberts Rhinehart and Mrs. J. Coggeshal, and all the active commercial fishermen of the Spearing family.

As this study progressed many other items of ichthyological interest appeared incidentally. Those pertinent to the study of the tarpon itself which have been published follow: Breder (1939a, b and c, 1940a, 1942e), Shlaifer (1941), Shlaifer and Breder (1940). Publications on other subjects directly derived from the work of this field station are as follows: Bishop

(1940), Breder (1939d, 1940b and c, 1941a, b and c, 1942a, b, c and d, 1943 and 1944 Breder and Springer (1940), Breder and Krumholz (1941 and 1943), Cox and Breder (1943), Gregory and Conrad (1943), Merriman (1940), Storey (1940). Numerous other items are in press or still under study.

Activity at the field station covered various periods, as needs demanded and the press of other matters permitted. From 1938 up to and including 1942, parts of each year were spent in field work. Most of this occupied the spring and summer months so as to cover the tarpon spawning season.

#### THE HABITAT OF TARPON.

Tarpon are known mostly in their larger sizes. In lengths mostly upward of three feet they are generally to be found in coast-wise waters not far from shore and most frequently in inlets, estuaries and passes between islands. Sometimes they may be found well up rivers and frequently they enter fresh waters for considerable distances. They are not normally found in the open ocean at any great distance from shore.

Fish under two feet in length are only rarely taken in such places as described above and those of considerably smaller sizes are known almost entirely from small bodies of water, and most frequently are land-locked when found. Such places may be a considerable distance from the sea-side. Otherwise the smaller sized fish are generally found well up rivers. In the vicinity of the place where this work was carried out, the Peace River and the Shark River are favored haunts of the species in its smaller sizes, although large fishes are often taken, especially in the lower reaches of the latter. Specimens may range down to sizes of a little over two inches in length. Below that their whereabouts is still a mystery and this item is discussed under a consideration of the larval tarpon. The finding of small tarpon has frequently been the subject of notices by the finder. Such are discussed by Evermann and Marsh (1902), Coker (1921a and b), Eigenmann (1921), Beebe (1927 and 1928), Beebe and Tee-Van (1928), Storey and Perry (1933) and Breder (1933, 1937, 1939b and c). All but one of these refer to the occurrences in land-locked or practically land-locked places. These they evidently enter from a previous existence in the sea, as indicated by Babcock (1936) and Breder (1939c), at times of temporary connections with open water. In one case Mr. Bishop actually saw them entering a newly storm-made cut which was again closed in a short time, securely land-locking these fishes. Of this case Breder (1939c) wrote:

"It has long been suspected that small tarpon may get into the odd places in which they are sometimes found by being driven in on the wings of a hurricane or late summer storm. Mr. Bishop was exceptionally fortunate in being in the field when two earlier-than-usual blows piled up the water into arms and other places that are seldom invaded by high water. Wherever there was such a connection with the sea Mr. Bishop plied his nets to see if the new ocean water brought anything in with it. Since he well knew from last season's work just what was in these places, he was in an excellent position to obtain a proper understanding of what was going on—if anything. Last year there were no such early storms and the places were either completely dry, or stagnant to such an extent that the only local species capable of survival was the air-breathing tarpon.

"Place after place was visited and nothing but the usual run of small shore fishes could be found in these freshly inundated pools. Mr. Bishop was about to give up and almost ready to invoke the old and feeble dodge of attributing the presence of fishes in odd places to wading birds carrying eggs adherent to their feet—only tarpon eggs are not sticky—when he came upon the last accessible place he knew about. This is on the south shore of Sanibel Island, near Point Ybel. Here, on overflowed land destined to become dry again shortly, he found his quest—tiny tarpon just as they entered these sequestered lagoons. The first time he saw this place it was still connected with the sea, but later was cut off and rapidly evaporating. These particular little tarpon were doomed to desiccation—or as Bishop puts it, before that, to be cleaned up by the abundant bird life when the water subsides a few inches, and before real desiccation commences. This would appear to be the frequent fate of many little tarpon every time they attempt to venture inland."

Such land-locked places vary considerably, some being actually more saline than the ocean, due to evaporation, while others may be practically fresh water. Frequently these pools are exceedingly foul and filled with decomposing organic matter and are of such a nature that other fishes cannot endure. Tarpon by virtue of their ability to breathe atmospheric oxygen survive easily in such places. The significance of these peculiarities of habitat plays an important part in an attempt to understand the nature of the growth of these fishes as will develop in the discussion of the interpretation of the markings on the scales. The anatomy of the lung-like swim bladder is discussed by Hildebrand in Babcock (1936) and its importance in respiration

by Shlaifer and Breder (1940), Shlaifer (1941) and Breder (1942e).

The occurrence of large tarpon in fresh water has been frequently noted. Such places as Lake Nicaragua, Simmons (1900), Gil (1907), and Miller (1936); the Chagres River, Panama, Meek and Hildebrand (1923), Breder (1925), Hildebrand (1937 and 1939), and Babcock (1936), are both famous for tarpon. Babcock gives an extended list of such places covering, in addition to the United States, Central America and the West Indies. He mentions reports of tarpon being found more than one hundred miles inland and the author has seen tarpon in the Rio Tampaon, near Pujal, S.L.P., Mexico, at a point which is considerably more than 100 miles from the sea as the river winds, while Dr. Myron Gordon reports having seen them in the Rio Tonto not distant from the town of Papaloapan, in the State of Oaxaca, Mexico, some eighty miles from the sea measured along the river. The ability of tarpon to live in fresh water is considerable, if not indefinite, and there are still living in a small fresh-water aquarium at the Bingham Oceanographic Laboratory, Yale University, several small specimens taken in 1938, with no indication of deterioration due to the nature of the water, during this period of six years.

#### BODY PROPORTIONS OF TARPON.

In order to be prepared to make as much use as possible of anglers' data, it became necessary to determine correlations between the various measures that have been used to measure tarpon. No single method is completely satisfactory, but the customary "standard length" is least objectionable for most ichthyological purposes. A series of specimens have been measured according to the several measurements in use by tarpon anglers. This material has been reduced to percentage of the standard length and is given in Table I. The various measurements as here understood may be defined as follows.

*Standard length.* The distance in a straight line from the tip of the snout to the caudal base.

*Total length.* Similar to the standard length but measured to the tip of the caudal fin in a "normal" expanded position.

*Overall length.* Similar to the standard length but measured to the tip of the caudal fin with the lobes pressed together.

*Length to fork.* Similar to standard length but measured to the tip of the shortest central caudal ray.

*Length including jaw.* Similar to overall length but measured from the tip of the lower jaw when the mouth is closed.

Aside from faulty tapes and poor techniques, there is considerable difficulty in obtaining accurate measurements of tarpon in the larger sizes. One of the sources of difficulty is the changes in length induced by stretching the fish as it is dragged about, generally by the lower jaw.

There is evidently only a slight amount of heterogony in the growth of these fishes but the somewhat changing relationships of the various measures of length is broken down in Table I into a series of size groups with which material may be compared. More of such measurements must be obtained, especially in the larger sizes, before a nomographic or other similar treatment would be warranted. Nevertheless this table can yield estimates from any one of the measurements that are of sufficient accuracy to give reasonably satisfactory estimates.

These figures have been based on wild fish exclusively, for it has been found that specimens kept in aquaria for long periods showed a tendency for the tail to grow proportionally longer. This condition is possibly related to lack of vigorous swimming enforced on such specimens. Due to the fish's efforts to swim through the glass, sometimes continual, an effort carried on longer in this species than in any other known to the author, there frequently results a deformation of the jaw, which, while not apparently inconveniencing the fish, further modifies the relations of its longitudinal proportions.

The weight-length relationships of tarpon need many more data to be worked out in a thoroughly satisfactory manner. Normally tarpon are slab-sided fish, relatively light in weight for their length, but during the spawning season the females may increase considerably in weight. Although anglers like to weigh their fish, it is probably the least satisfactory measure for any analytical study and little, of use in present connections, can be done with catch records that give weight only. This is further complicated by the fact that in the warm climates in which the tarpon is found, the weight of the fish changes considerably after lying around in boats or on docks for variable periods, sometimes wet and sometimes dry. Babcock (1936) discusses this at length. He gives a formula showing the relationship of length and weight, in which the girth of the fish is taken into account. At this writing we are unable to improve on the accuracy of this purely empirical expression and probably it is adequate to the present uncertain nature of the variations that come into any measurement made on large tarpon. The formula which Babcock (1936) gives may be expressed as follows.

TABLE I. COMPARISON OF MEASURES OF LENGTH IN TARPON ACCORDING TO SIZE GROUPS.  
Number of specimens precedes each measurement in parenthesis.  
Dimensions expressed as per cent. of standard lengths.

[Range]	STANDARD LENGTHS IN CM.			TOTAL LENGTHS			OVERALL LENGTHS			LENGTHS TO FORK			LENGTHS INC. JAW		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
5-6	(47)	5.0	5.4	5.9	129.3	131.5	134.0	(13)	129.3	131.5	134.0	(5)	133.0	134.9	(5)
6-7	(7)	6.0	6.2	6.7	128.2	128.4	128.7	(2)	128.2	128.4	128.7	(1)	127.4	127.4	(1)
7-8	(17)	7.0	7.6	7.9	126.9	127.0	127.4	(10)	126.9	127.0	127.4	(16)	126.9	127.0	(16)
8-9	(26)	8.0	8.5	8.9	126.9	127.0	127.4	(16)	126.9	127.0	127.4	(10)	126.9	127.0	(10)
9-10	(26)	9.0	9.4	9.8	126.9	127.0	127.4	(16)	126.9	127.0	127.4	(10)	126.9	127.0	(10)
10-11	(9)	10.0	10.5	10.9	126.9	127.0	127.4	(4)	126.9	127.0	127.4	(4)	126.9	127.0	(4)
11-12	(7)	11.0	11.4	11.9	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
12-13	(5)	12.1	12.4	12.9	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
13-14	(3)	13.7	13.8	13.9	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
14-15	(2)	14.2	14.3	14.4	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
15-16	(2)	15.0	15.2	15.3	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
17-18	(2)	17.0	17.1	17.1	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
58-59	(1)	58.4	58.4	58.4	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
61-62	(2)	61.0	61.3	61.6	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
118-119	(1)	118.1	118.1	118.1	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
123-124	(1)	123.1	123.1	123.1	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
125-126	(1)	125.8	125.8	125.8	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
141-142	(1)	141.0	141.0	141.0	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
146-147	(1)	146.8	146.8	146.8	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
149-150	(1)	149.8	149.8	149.8	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
188-189	(1)	189.0	189.0	189.0	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)
193-194	(2)	193.0	193.9	194.9	126.9	127.0	127.4	(2)	126.9	127.0	127.4	(2)	126.9	127.0	(2)
202-203	(164)	202.8	202.8	202.8	126.9	127.0	127.4	(1)	126.9	127.0	127.4	(1)	126.9	127.0	(1)

$$W = \frac{G^2 \times L}{800}$$

In which: G = girth in inches, L = total length in inches, W = weight in pounds.

Measurements of length and weight of number of specimens caught by Mr. Bishop are given in Table II, together with some other data culled from the literature and converted to the same standards. These data indicate a considerable variation in weight for a given size, which feature shows clearly in the graphic presentation of Text-figure 1 and emphasizes the utility of the girth factor in the formula of Babcock. Unfortunately many measurements of others were necessarily discarded because of obvious difficulties in interpreting the nature of the "length" measurement.

The exponential length-weight ratio in fishes has been discussed by Hecht (1916), Hile (1931), Shapiro (1943) and others. The derivation of a formula expressing this ratio within reasonable limits of size may be found in any of the above. While it is generally applicable to fishes, it naturally gives a much closer approximation in those

TABLE II. LENGTH AND WEIGHT OF TARPON.  
Measurements taken by M. B. Bishop unless otherwise indicated.

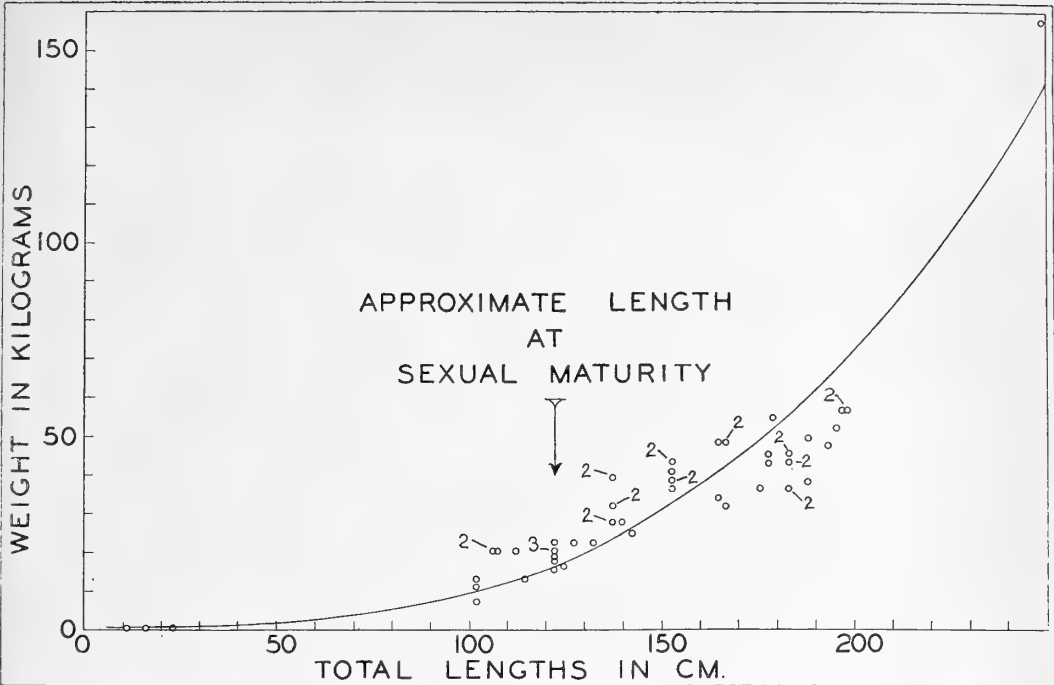
TOTAL LENGTHS IN CM.	WEIGHT IN KG.	TOTAL LENGTHS IN CM.	WEIGHT IN KG.
10.0	0.0050 <sup>2</sup>	139.9	27.215
10.8	0.0105 <sup>1</sup>	142.2	24.947
16.3	0.0125 <sup>1</sup>	152.5	36.287
23.2	0.0650 <sup>2</sup>	152.5	38.555
76.3	18.143	152.5	43.091
101.5	11.339	152.5	40.823
101.5	13.607	152.5	43.091
101.5	7.711	152.5	38.555
106.6	20.411	165.0	40.832
106.6	20.411	165.0	34.019
107.0	20.411	167.5	40.823
111.8	11.339	167.5	31.751
114.1	13.607	167.5	40.823
122.0	15.875	175.5	36.287
122.0	22.679	178.0	45.359
122.0	20.411	178.0	43.091
122.0	18.143	179.0	54.430
122.0	20.411	183.0	43.091
122.0	15.875	183.0	43.091
122.0	19.050	183.0	54.430
122.0	20.411	183.0	36.287
124.5	16.329 <sup>3</sup>	183.0	36.287
127.0	22.679	183.0	45.359
132.0	22.679	188.0	49.849
137.0	31.751	188.0	38.500
137.0	31.751	193.0	47.626
137.0	27.215	195.5	52.162
137.0	27.215	197.0	56.698
137.0	29.483	197.0	56.698
137.0	39.462	198.0	56.698
		249.0	158.756

<sup>1</sup> From Storey and Perry (1933).

<sup>2</sup> From Beebe and Tee-Van (1928).

<sup>3</sup> From Babcock (1936).

<sup>4</sup> From Breder (1925).



TEXT-FIG. 1. Length and weight relationships of tarpon. Based on data of Table II. Solid line represents best fit of the exponential relationship of length and weight. See

text for full explanation for formula 
$$W = \frac{0.9 L^3}{100,000}$$

which show only slight heterogonic growth characteristics, than in those displaying large proportional changes with increasing size. Since the tarpon is conspicuously one of the former, as is indicated by the measurements of Table III, it should be expected to subscribe to such a formula in a reasonably satisfactory manner.

The basic formula states that the weight varies directly as the cube of the length, as follows:

$$\frac{W}{L^3} = c \text{ or } W = cL^3$$

where W = weight, L = length and c = an empirical constant derived from the above formula and differing for each species dependent on its characteristic slimness or rotundity. When the measurements are expressed in the metric system, it is convenient to introduce another constant, k, where if, as in the present case, the measurements have been made in centimeters and kilograms:

$$\frac{k}{100,000} = c$$

This then yields the equation:

$$W = \frac{kL^3}{100,000}$$

Since it has been found by purely empirical means that for tarpon the value of k giving the closest fit to the data at hand is 0.9, the working expressions become:

$$W = \frac{0.9 L^3}{100,000} \text{ and } L = \sqrt[3]{\frac{100,000 W}{0.9}}$$

when weight is expressed in kilograms and length in centimeters.

This equation may be most conveniently transformed for use with inches and pounds in the following manner: L is multiplied by 2.54, the number of cms. in an inch, and W is multiplied by 0.45359, the number of kilos. in a pound. The expressions then become as follows:

$$0.45359 W = \frac{0.9(2.54L)^3}{100,000} \text{ or } W = \frac{(2.54L)^3}{50,400} \text{ and } L = \frac{\sqrt[3]{50,400 W}}{2.54}$$

These, of course, could be transformed in other ways but the above is perhaps as convenient as any.

Some of the deviations from the mean in the present data are fairly large, as indicated in Text-figure 1, but probably have more to do with individual variation, associated with the sex and the fatness of

TABLE III—CHANGE OF PROPORTIONS IN RELATION TO SIZE IN TARPON.  
Number of specimens precedes each measurement in parenthesis.  
Dimensions expressed as per cent of standard lengths.

Range	STANDARD LENGTHS IN CM.			HEAD			DEPTH			SNOUT			ORBIT		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
5-6 (47)	5.0	5.4	5.9	(34)	30.0	31.3	33.0	(38)	23.1	25.0	26.9	(37)	5.8	6.9	9.3
6-7 (7)	6.0	6.2	6.7	(7)	30.2	30.9	32.0	(6)	24.3	25.3	26.3	(7)	6.4	7.1	9.2
7-8 (17)	7.0	7.6	7.9	(16)	28.9	30.4	32.9	(15)	20.9	23.3	25.4	(17)	5.7	6.7	7.5
8-9 (26)	8.0	8.5	8.9	(25)	27.9	30.0	32.6	(12)	23.6	25.1	26.6	(24)	5.6	6.4	6.7
9-10 (26)	9.0	9.4	9.8	(26)	27.2	29.3	30.6	(25)	22.2	24.4	26.2	(25)	5.4	6.0	6.5
10-11 (9)	10.0	10.5	10.9	(9)	27.3	28.4	29.3	(9)	20.9	25.1	26.4	(9)	5.2	6.0	6.5
11-12 (7)	11.0	11.4	11.9	(7)	26.8	28.5	29.8	(7)	21.8	24.4	27.0	(7)	5.8	6.0	6.5
12-13 (5)	12.1	12.4	12.9	(5)	25.6	27.6	28.9	(5)	22.6	24.0	25.4	(5)	5.4	5.9	6.5
13-14 (3)	13.7	13.8	13.9	(3)	24.1	26.2	27.7	(3)	24.9	25.5	25.9	(3)	5.5	5.9	6.2
14-15 (2)	14.2	14.3	14.4	(2)	26.2	26.5	26.8	(2)	22.2	23.1	24.0	(2)	5.5	5.7	5.8
15-16 (2)	15.0	15.2	15.3	(2)	27.0	27.1	27.2	(2)	24.1	24.2	24.2	(2)	5.2	5.6	6.0
17-18 (2)	17.0	17.0	17.1	(2)	26.8	26.8	26.8	(2)	21.8	23.1	24.4	(2)	5.6	5.6	5.6
58-59 (1)	—	58.4	—	(1)	—	21.8	—	—	—	—	—	(1)	—	4.6	—
61-62 (2)	61.0	61.3	61.6	(2)	22.1	22.5	23.0	—	—	—	—	(2)	4.3	4.5	4.6
146-147 (1)	—	146.8	—	(1)	—	22.8	—	—	—	—	—	(1)	—	4.0	—
188-189 (1)	—	189.0	—	(1)	—	24.5	—	—	—	—	—	(1)	—	3.6	—
193-194 (2)	193.0	193.5	194.9	(2)	21.5	22.0	22.4	—	—	—	—	(2)	3.5	3.5	3.6
202-203 (1)	—	202.8	—	(1)	—	23.3	—	—	—	—	—	(1)	—	3.6	—
(164)								(126)				(143)			(152)

Range	STANDARD LENGTHS IN CM.			MAXILLARY			INTERORBITAL			DORSAL ORIGIN			ANAL		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
5-6 (47)	5.0	5.4	5.9	(36)	17.1	18.6	20.2	(40)	3.6	5.5	6.3	(38)	50.6	54.0	50.8
6-7 (7)	6.0	6.2	6.7	(7)	17.9	18.5	20.0	(7)	4.7	5.3	5.7	(6)	51.5	52.8	55.9
7-8 (17)	7.0	7.6	7.9	(16)	17.3	18.3	19.5	(17)	4.8	5.4	5.7	(16)	52.5	54.7	56.7
8-9 (26)	8.0	8.5	8.9	(24)	16.8	18.2	19.4	(24)	4.9	5.5	6.4	(25)	51.3	53.5	56.6
9-10 (26)	9.0	9.4	9.8	(26)	16.4	17.6	18.5	(25)	4.8	5.4	5.8	(25)	52.4	53.7	56.2
10-11 (9)	10.0	10.5	10.9	(9)	16.7	17.4	17.8	(9)	5.1	5.3	6.0	(9)	51.0	53.7	55.8
11-12 (7)	11.0	11.4	11.9	(7)	16.0	17.5	17.7	(7)	5.2	5.5	5.9	(7)	51.2	53.1	54.8
12-13 (5)	12.1	12.4	12.9	(5)	16.3	17.0	17.8	(5)	4.9	5.6	5.7	(5)	50.8	53.0	54.3
13-14 (3)	13.7	13.8	13.9	(3)	16.3	16.2	17.2	(3)	5.1	5.5	6.2	(3)	51.8	53.3	55.5
14-15 (2)	14.2	14.3	14.4	(2)	16.1	16.2	16.3	(1)	—	4.8	—	(2)	53.9	54.5	54.5
15-16 (2)	15.0	15.2	15.3	(2)	16.0	16.1	16.1	(2)	4.7	5.2	5.7	(2)	54.8	54.9	55.0
17-18 (2)	17.0	17.0	17.1	(2)	16.4	16.7	17.0	(2)	5.2	5.4	5.5	(2)	53.0	53.1	53.4
58-59 (1)	—	58.4	—	(1)	—	13.2	—	—	—	—	—	(1)	—	56.4	—
61-62 (2)	61.0	61.3	61.6	(2)	12.6	12.9	13.1	(2)	4.6	4.6	4.6	(2)	54.2	54.9	55.6
146-147 (1)	—	146.8	—	(1)	—	13.4	—	—	—	—	—	(1)	—	51.6	—
188-189 (1)	—	189.0	—	(1)	—	13.5	—	—	—	—	—	—	—	—	—
193-194 (2)	193.0	193.5	194.9	(2)	12.7	12.8	12.9	—	—	—	—	—	—	—	—
202-203 (1)	—	202.8	—	(1)	—	12.4	—	—	—	—	—	—	—	—	—
(164)								(144)				(144)			(144)



TABLE III (CONTINUED)—CHANGE OF PROPORTIONS IN RELATION TO SIZE IN TARPON.

Number of specimens precedes each measurement in parenthesis.  
Dimensions expressed as per cent of standard lengths.

STANDARD LENGTHS IN CM.			PECTORAL INSERTION			VENTRAL INSERTION			DORSAL BASE			ANAL BASE					
Range	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.		
5-6 (47)	5.0	5.4	5.9	(38)	28.6	30.9	33.6	(38)	49.2	52.2	54.2	(38)	8.7	10.2	11.9		
6-7 (7)	6.0	6.2	6.7	(7)	29.4	31.2	32.6	(7)	50.5	51.9	53.2	(7)	9.1	10.2	11.2		
7-8 (17)	7.0	7.6	7.9	(16)	27.8	29.9	34.1	(16)	46.2	50.1	52.2	(15)	8.2	9.4	10.4		
8-9 (26)	8.0	8.5	8.9	(24)	26.8	29.9	33.2	(24)	43.7	50.1	52.6	(24)	8.5	9.7	11.1		
9-10 (26)	9.0	9.4	9.8	(25)	27.5	29.0	34.6	(26)	46.8	48.7	52.0	(25)	8.4	9.2	11.3		
10-11 (9)	10.0	10.5	10.9	(9)	27.1	28.1	29.7	(9)	46.3	48.2	50.5	(8)	8.4	9.3	10.1		
11-12 (7)	11.0	11.4	11.9	(7)	25.8	28.1	29.4	(7)	46.3	48.3	52.1	(7)	9.0	9.7	10.7		
12-13 (5)	12.1	12.4	12.9	(5)	26.0	27.3	28.2	(5)	45.2	47.2	49.6	(5)	9.5	10.0	10.6		
13-14 (3)	13.7	13.8	13.9	(2)	25.9	27.1	28.3	(3)	47.5	48.2	49.2	(3)	8.8	9.1	9.5		
14-15 (2)	14.2	14.3	14.4	(2)	25.3	26.0	26.6	(2)	45.1	45.6	46.1	(2)	9.4	9.5	9.6		
15-16 (2)	15.0	15.2	15.3	(2)	26.3	26.4	26.4	(2)	46.0	46.9	47.9	(2)	8.5	8.6	8.7		
17-18 (2)	17.0	17.0	17.1	(2)	26.8	26.9	27.0	(2)	47.8	48.3	48.8	(2)	9.1	9.3	9.5		
58-59 (1)	—	58.4	—	(1)	—	21.0	—	(1)	—	42.4	—	(1)	—	9.4	—		
61-62 (2)	61.0	61.3	61.6	(2)	21.4	21.5	—	(2)	41.2	43.0	44.7	(2)	9.0	9.4	9.7		
146-147 (1)	—	146.8	—	(1)	—	28.8	—	(1)	—	42.2	—	(1)	—	18.5	18.6		
188-189 (1)	—	189.0	—	(1)	—	—	—	(1)	—	—	—	(1)	—	—	—		
193-194 (2)	193.0	193.5	194.9	(2)	—	—	—	(2)	—	—	—	(2)	—	—	—		
202-203 (1)	—	202.8	—	(143)	—	—	—	(145)	—	—	—	(141)	—	—	—		
(164)																	
STANDARD LENGTHS IN CM.			PECTORAL LENGTH			VENTRAL LENGTH			LAST DORSAL RAY			DORSAL HEIGHT			ANAL HEIGHT		
Range	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.		
5-6 (47)	5.0	5.4	5.9	(36)	18.3	19.9	23.0	(36)	15.9	17.2	19.4	(38)	8.5	10.3	13.0		
6-7 (7)	6.0	6.2	6.7	(7)	18.8	19.8	20.2	(7)	15.6	15.2	17.4	(7)	9.1	10.2	11.3		
7-8 (17)	7.0	7.6	7.9	(11)	19.7	20.3	20.9	(13)	16.2	17.0	18.7	(16)	8.6	11.6	14.1		
8-9 (26)	8.0	8.5	8.9	(20)	18.1	20.0	22.4	(20)	15.0	16.6	18.4	(22)	7.8	11.4	15.3		
9-10 (26)	9.0	9.4	9.8	(21)	18.4	20.0	22.1	(21)	14.9	16.1	17.2	(25)	7.8	10.4	14.2		
10-11 (9)	10.0	10.5	10.9	(6)	16.7	18.7	20.4	(5)	15.0	15.8	16.6	(6)	7.8	10.1	14.1		
11-12 (7)	11.0	11.4	11.9	(4)	17.9	19.9	21.7	(5)	14.2	15.2	16.3	(7)	8.2	10.9	14.4		
12-13 (5)	12.1	12.4	12.9	(2)	18.3	18.9	19.5	(2)	15.3	16.9	18.6	(4)	7.7	10.0	13.3		
13-14 (3)	13.7	13.8	13.9	(3)	19.0	19.6	20.5	(3)	14.5	14.7	15.0	(2)	8.0	8.2	8.3		
14-15 (2)	14.2	14.3	14.4	(2)	19.2	19.5	19.7	(2)	—	—	—	(2)	7.8	11.8	15.8		
15-16 (2)	15.0	15.2	15.3	(2)	18.5	18.8	19.0	(2)	12.7	13.2	13.7	(1)	—	—	—		
17-18 (2)	17.0	17.1	17.1	(1)	—	16.6	—	(2)	12.2	13.0	13.8	(1)	—	—	—		
58-59 (1)	—	58.4	—	(2)	15.0	15.7	16.2	(1)	—	11.9	—	(1)	—	17.9	—		
61-62 (2)	61.0	61.3	61.6	(2)	—	—	—	(2)	10.7	11.1	11.7	(2)	19.5	19.9	20.3		
146-147 (1)	—	146.8	—	(117)	—	—	—	(119)	—	—	—	(134)	—	—	—		
188-189 (1)	—	189.0	—	(1)	—	—	—	(1)	—	—	—	(1)	—	—	—		
193-194 (2)	193.0	193.5	194.9	(2)	—	—	—	(2)	—	—	—	(2)	—	—	—		
202-203 (1)	—	202.8	—	(1)	—	—	—	(1)	—	—	—	(1)	—	—	—		
(164)																	
														(28)	17.6	20.0	22.6
														(6)	18.2	19.9	20.9
														(6)	18.6	20.0	20.8
														(17)	17.1	19.3	21.7
														(21)	13.6	18.6	20.5
														(6)	14.7	18.4	20.5
														(4)	18.0	18.7	19.9
														(2)	19.0	20.7	22.5
														(3)	17.2	17.7	18.8
														(1)	—	—	—
														(2)	13.3	—	—
														(1)	—	14.3	—
														(1)	—	16.2	—
														(2)	14.7	15.0	15.2
														(1)	—	—	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	18.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3
														(1)	—	—	—
														(2)	20.3	—	—
														(2)	19.3	20.9	22.2
														(2)	19.5	20.2	20.9
														(3)	20.2	20.4	20.5
														(1)	—	20.3	—
														(2)	13.9	20.1	21.3
														(2)	19.5	19.9	20.2
														(1)	—	17.9	—
														(2)	16.1	16.1	16.3</

the specimens than with gross errors of measurement. The latter item, the term "condition" of fisheries biologists, to which k is sometimes referred as the "coefficient of condition," would appear to be markedly variable in this species, a matter which field observation on the evident plumpness or leanness of individual specimens tends to support.

Since tarpon are not used for food, large numbers are not collected by commercial agencies, and since most anglers return their catches to the water, on a conservation basis, it is difficult to obtain large series of specimens for careful measurement. It is clear that sex and condition play an important role in the length-weight relationship of these fishes. If enough material with the sex known could be obtained, it would go far toward making possible the development of a more accurate expression of this relationship.

Probably for reasons similar to those mentioned above, surprisingly few taxonomic measurements on this fish have found their way into the literature. To help remedy this condition a series of 164 specimens was measured, covering the usual taxonomic measurements and some less usual. These are given in Table III. In a manner identical with Table I, the data have been broken up into size groups to indicate more certainly the slight variations in proportions that these fish undergo with growth. This was necessary, in addition, to separate clearly the smaller size groups, which have never been measured in any adequate manner before. Small tarpon, down to the smallest sizes in this series, resemble the large adults to a most remarkable degree. The only conspicuous difference, other than the slight shifts in various proportions, is the great elongation of the last dorsal ray shown by the larger specimens. In the smallest material this is scarcely longer than the next to the last ray, showing as a mere "point" at the end of the fin. It varies from a mean of about 10% of the standard length in the smallest to well over 20% in really large fish. The rather large amount of variation in the length of this ray, as indicated in Table III, is evidently due to mutilation and regeneration. Perhaps the maximum length it attains, rather than the mean, would be a better measure of the normal length of this element.

The meristic counts have fared no better in the literature. Table IV is a similar attempt to supply an adequate series of such measurements. The lateral series and the predorsals are shown comparatively. The most frequent occurrence is 44 in lateral scales and 24 predorsal scales. The cluster-

TABLE IV. COMPARISON OF TARPON SCALE AND FIN RAY COUNTS.

SCALES OF TARPON (71 specimens)							
Predorsal scales	Lateral line scales						totals
	42	43	44	45	46	47	
21	1	2	1	—	—	—	4
22	1	—	7	5	2	—	15
23	—	7	1	4	—	—	12
24	1	4	9	8	3	1	26
25	—	2	3	6	1	—	12
26	—	—	1	1	—	—	2
totals	3	15	22	24	6	1	71

FIN RAYS OF TARPON <sup>1</sup> (139 specimens)						
Dorsal fin	23	24	25	26	27	totals
15	—	2	—	—	2	4
16	1	12	20	20	18	71
17	—	4	29	21	10	64
totals	1	18	49	41	30	139

<sup>1</sup> All rays counted as one. See text for explanation.

ing of the scatter about this point is evident. The arithmetic means are 44.3 and 23.5 respectively.

The method of counting the fin rays in tarpon is evidently a matter that has led to some difficulty. As usually rendered in taxonomic descriptions, they appear as three or four less in both dorsal and anal counts than given in Table IV. In large fish the first four or five are consolidated into a solid leading edge, which have generally been counted as one ray. In the smallest sizes the separation of these rays is evident and doubtless, if small fish instead of large were generally available to taxonomists, the usage would have developed differently. In both anal and dorsal fins the rays, as here counted, appear as distinct when sufficiently prepared. The most frequent occurrence is 16 dorsal and 25 anal rays, as here counted. The arithmetic means are 16.4 and 25.5 respectively. The method of counting these fin rays has a curious bearing on the postlarval fish, which is discussed under that head. Taxonomic measurements taken from the literature are given comparatively in Table V. It is evident from this table that only Fowler (1936) gave the full dorsal and anal counts, indicating the number of consolidated rays by lower case roman numerals. Various other taxonomic characters not otherwise discussed herein are also given in this table.

#### LARVAL AND POSTLARVAL TARPON.

Tarpon in sizes below that at which they take on essentially the appearance of the adults are still not known with certainty. During these studies efforts were made to strip and fertilize the eggs of ripe speci-

TABLE V. TARPON COUNTS AND MEASUREMENTS FROM RECENT LITERATURE.  
All measurements given in per cent. of standard length except as otherwise noted.

AUTHORITY	DORSAL	ANAL	L.L. <sup>1</sup>	P.D. <sup>2</sup>	OVER L.L.	UNDER L.L.	GILL-RAKERS	BR. <sup>3</sup>
Jordan & Evermann (1897)	12	20	42	—	—	—	—	—
Smith (1907)	12	20-23	Circa 45	—	—	12	—	23
Meek & Hildebrand (1923) and Hildebrand & Schroeder (1928)	12-15	20-23	42-47	—	—	—	? + 32-36	—
Beebe & Tee-Van (1928)	14	22	—	—	—	—	—	—
Nichols (1929)	12	19-20	42	—	—	—	—	—
Beebe & Tee-Van (1933)	12-15	19-23	42-47	—	—	—	—	—
Fowler (1936)	iv-v, 10-11	iv-v, 18-19	40-43 + 2-3	20-23	5	5-6	Circa 26 <sup>7</sup> + 39	—
Present data	15-17	23-27	42-47	21-26	4	6	16-19 + 35-37	—
No. of specimens	(139)	(139)	(71)	(71)	(76)	(76)	(2)	—
AUTHORITY	HEAD	DEPTH	SNOUT	ORBIT	MAXILLARY	INTERORBIT.	PECTORAL LENGTH	LAST DORSAL RAY
Jordan & Evermann (1897)	25 <sup>4</sup>	25 <sup>4</sup>	—	16 <sup>5</sup> 66 <sup>5</sup>	—	—	—	—
Smith (1907)	23 3-24.4	26.0-29.4	19.6-20.8 <sup>5</sup>	21.5-25.6 <sup>5</sup>	58.8-66.6 <sup>5</sup>	—	6.2-9.2 <sup>5</sup>	—
Meek & Hildebrand (1923) and Hildebrand & Schroeder (1928)	22 6-28.2	24.2-25.8	6.2-7.4	4.1-7.8	14.0-16.7	—	19.1-20.5	10.2-27.1
Beebe & Tee-Van (1928)	25	26.3-27.0	—	22.2-22.7 <sup>5</sup>	—	—	—	—
Nichols (1929)	22.7-25.0	26.0-29.4	19.6-20.8 <sup>5</sup>	21.5-25.6 <sup>5</sup>	58.8-67.7 <sup>5</sup>	—	—	—
Beebe & Tee-Van (1933)	25.0-30.8	22.2-27.3	19.6-20.4 <sup>5</sup>	21.5-29.4 <sup>5</sup>	57.0-60.0 <sup>5</sup>	18.2-20.0 <sup>5</sup>	—	—
Fowler (1936)	20.9-27.0	20.9-27.0	4.3-9.3	3.5-8.9	12.6-20.2	3.6-6.3	15.0-23.0	7.7-20.3
Present data	(146)	(126)	(143)	(152)	(147)	(144)	(117)	(134)
No. of specimens								

<sup>1</sup> Lateral line  
<sup>2</sup> Predorsal scales  
<sup>3</sup> Branchiostegal rays  
<sup>4</sup> Per cent of total length  
<sup>5</sup> Per cent of head  
<sup>6</sup> Per cent of snout  
<sup>7</sup> Probably a misprint for 16

mens. Males with running milt were obtained without difficulty but it was found impossible to obtain females with eggs in a sufficiently advanced stage to enable successful fertilization to be accomplished. It is true that anglers often take females from which eggs are running and which give the superficial appearance of being mature. Microscopic examination, however, shows that they are not entirely ripe and experiments have demonstrated that they are not yet ready for fertilization. Evidently the vigorous contortions that these fishes make on being boated cause a premature expulsion of the roe in well distended females approaching ripeness. It is possible, and not unlikely, that females thoroughly ripe do not feed until after spawning. Sexual maturity is reached in this region at a total length of about four feet (122 cm.). The smallest ripe female seen was 139.8 cm. on July 3. A fish with fully undeveloped gonads of 142.2 cm. t. l. was taken on June 22. This was the largest sexually immature specimen examined. See indication of this in Text-figure 1. At this size they weigh close to 20 kilograms.

Since, during May, June and July at least, these fishes do spawn in the region as has been repeatedly observed in shallow water between the numerous islands, the eggs should be recoverable in tow-nets. Often pairs or three fish, evidently two males and one female, may be seen milling around, usually in water shallow enough to cause them to rile up the sand to a considerable extent. During this procedure white streaks or clouds appear, which are almost surely composed of quantities of milt emitted by the males. This was noted by Storey and Perry (1933) from near Sanibel and is in essential agreement with these personal observations. The sand pits described by Babcock (1936) may well be produced by spawning tarpon. Several were seen close to areas of unusual activity.

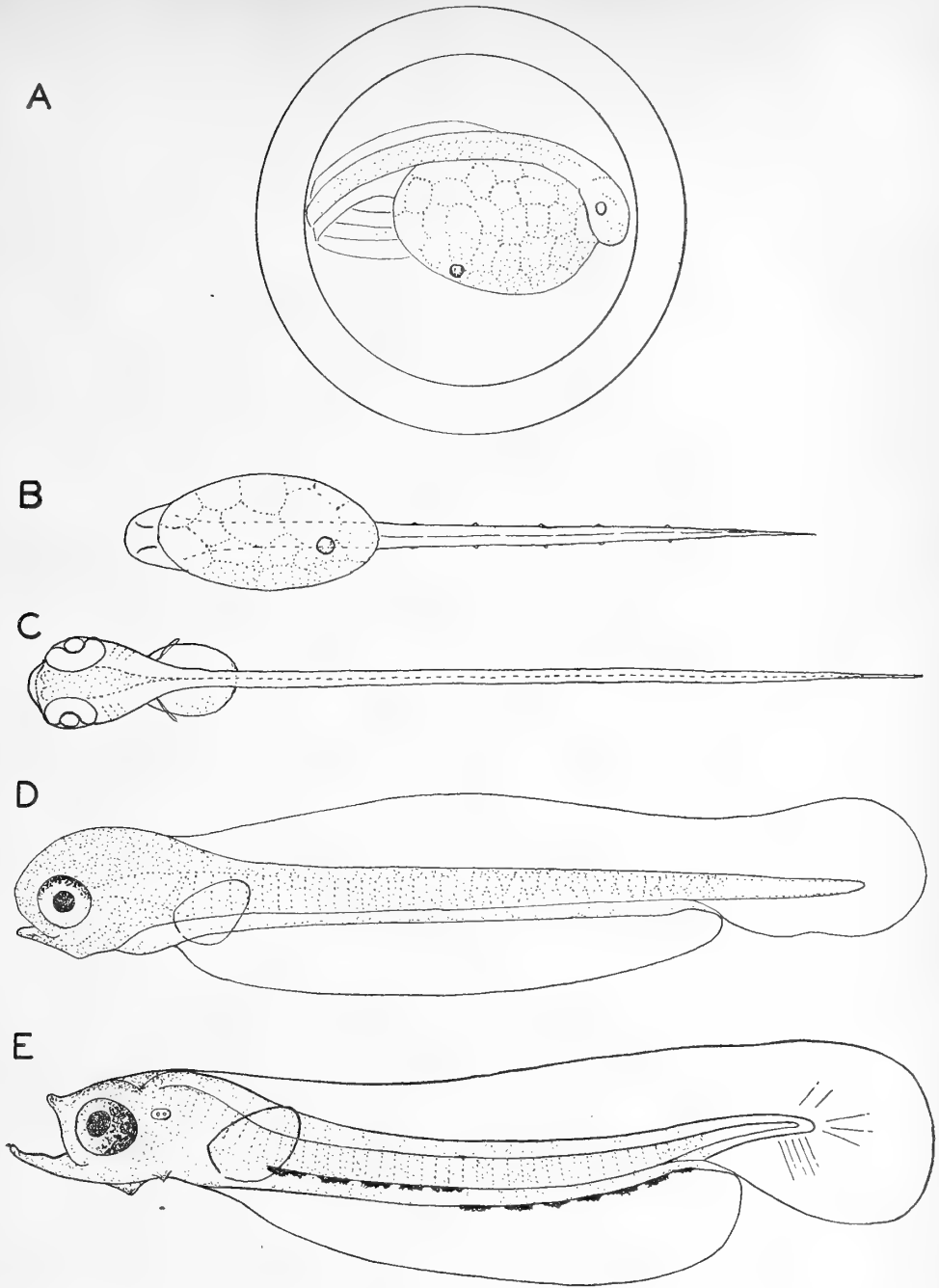
Tow-net operations at the surface have yielded no eggs that by any stretch of the imagination could be the eggs of tarpon as compared with the nearly ripe eggs taken from specimens. In this connection it was noted that these nearly ripe eggs sank in sea water even after they had water hardened, a fact first reported by Babcock (1936). Taking this as a hint, towing was undertaken close to the bottom in places near where tarpon were spawning. This method yielded very few eggs of any kind, but among them was one type that we have been unable to eliminate as clearly not that of the tarpon. Many such, in the aggregate, were taken during the years from 1938 to 1942 during the known spawning time of this species. Such an egg is shown in Text-

figure 2, a. If this is not the egg of the tarpon it is surprisingly like what the nearly ripe eggs must approach on full development. These eggs averaged a little less than 2 mm. (1.8 mm.) in diameter. This compares with nearly ripe ovarian eggs which, when water-hardened, averaged nearly this size. Babcock (1936) gives 0.6 to 0.75 mm. for preserved ripe ovarian eggs, which agrees well with our data on the above. The eggs taken by tow-net sank in the sea water in which found, which had a specific gravity of 1.0140 at 25°. They just about floated in the denser off-shore water, where, in fact, eggs could sometimes be taken at the surface tows. They were, however, too disperse to collect in any numbers by the means available.

These eggs were hatched and carried on into larval development as far as was possible in the laboratory. The longest any were successfully held in a viable state even under elaborate care was a matter of three days. The various stages that these pass through up to that time are shown in Text-figure 2. The egg shown measured 1.7 mm. in diameter. The details of the other stages passed through are given in the legend to Text-figure 2. It will be noted that the most advanced stage shows characters not unlike those seen in the pre-leptocephalid larvae of apodal fishes and also that there has been considerable shrinkage in the length of the last two stages. Whether this is associated with its evident consolidation or is associated with unsatisfactory conditions in the laboratory bowls is uncertain.

There was more than the usual difficulty in rearing these larvae for reasons additional to their own delicacy. It so happens that the shore waters of this region are extremely rich in plankton, as has already been noted by Breder and Krumholz (1943). In fact, it is so rich that a glassful dipped from sea at the end of the laboratory dock looks slightly turbid and if held up to the light can be seen to be full of "jumping" minute crustacea. Some of these are extremely voracious and prey on the newly hatched fish from the numerous kinds of planktonic eggs. It was soon found impossible to rear anything hatched from such eggs without placing them in water that had been first filtered through cotton, for only a single organism was necessary to ruin a bowl of hatchlings.

It was noted that in these tows there was never any fish life except unhatched eggs and fairly large postlarvae. Knowing the time of hatching of numerous species, tows made at that time would sometimes yield shells, but never recognizable larvae. This was carefully checked on the easily recognizable and abundant eggs of *Anchoa mitchilli* (Cuvier and Valenciennes). These



TEXT-FIG. 2. Development of larval fish from an egg which may be that of *Tarpon atlanticus*. **A.** An egg as taken from tow-net catches made near the bottom, 1.7 mm. dia. **B.** Ventral view of a larva at the time of hatching, 3.0 mm. long. At this time they float passively in an inverted position. **C.** Dorsal view of a larva 24 hours from the time of hatching, 3.9 mm. long. By this time they have righted themselves and are active. **D.** Lateral view of a larva 43 hours from the time of hatching, 2.9 mm. in length. The eye has become pigmented, the yolk is nearly gone and the mouth is open and functioning and shrinkage has commenced. **E.** Lateral view of a larva 72 hours from the time of hatching, 1.9 mm. in length. Two series of chromatophores have appeared ventrally, the otic sapsule is evident and the eyes have become inclined somewhat forward. The gape has reached considerable size and the behavior is voracious. The general appearance approaches that of the pre-leptocephalus of apodal fishes.

are elliptical and even the empty shells may be recognized at once. This condition was found to be uniformly true for any of the species with which we were sufficiently familiar to make such determinations without difficulty. In the same tows would be found large numbers of the postlarvae in the sizes studied by Breder and Krumholz (1943). No variations from this condition were found in tows made in the "green" shore waters. However, when tows were made in the outside "blue" Gulf waters, the newly hatched larvae were taken in abundance. The chief obvious difference between these two colors of water is the relative abundance of plankton, the blue waters representing relatively "desert" conditions. Evidently most of the local species of pelagic egg producers spawn both within the blue and green waters, the delimitations of which make a surprisingly sharp line. Consequently it is deduced from this fact and the experiments with filtered water in the laboratory that few, if any, eggs hatching within the limits of the "passes" escape destruction on hatching. Those spawned in the blue waters evidently have a reasonable survival rate, because of the many fewer predators waiting for them, and it is evidently the postlarvae developing from these that work back into the inside waters at a size no longer vulnerable to the crustacean elements. Their presence there at this time, make the crustaceans their chief food, in turn. This leaves one with the conclusion that the spawning of such fishes in these shore waters is a complete peripheral wastage and that the only fishes successfully spawning, in Pine Island Sound, for example, are those which in some manner protect their young through this vulnerable stage from various planktonic elements. Checking through the species about which there is sufficient data, which fall within the latter categories, the following forms are listed together with their protective mechanism.

## FISH.

## PROTECTION.

- All Elasmobranchs  
 Much too large at birth or hatching  
*Bagre marinus* (Mitchill)  
*Galeichthys felis* (Linnaeus)  
 Oral incubators and with eggs and young too large at hatching and release.  
 All Cyprinodontidae  
 Too large and advanced at hatching.  
 All Poeciliidae  
 Too large and advanced at birth.  
*Strongylura notata* (Poey)  
*Hyporhamphus unifasciatus* (Ranzani)  
 Too large and advanced at hatching.  
 All *Syngnathus*  
 All *Hippocampus*  
 Too large and advanced on release from brood pouch.

## All Atherinidae

Too large and advanced on hatching.

*Bathygobius soporator*

(Cuvier and Valenciennes)

Protected by parent in a shell cavity remote from the pelagic crustaceans.

*Gobiosoma robustum* Ginsburg

Same as preceding.

*Opsanus beta* Goode and Bean

Same as preceding and in addition too large at hatching.

*Paraclinus marmoratus* (Steindachner)

Protected by parent in lumen or cavities of a sponge and remote from pelagic crustacea.

This list covers all species of which we have positive knowledge of spawning in the Sound, many, by their natures, being practically confined to such places. All the others, pelagic egg producers, are also found in outside waters. It would thus appear that fishes here have two possible courses in regard to reproduction. If producing pelagic eggs, hatching at an early time into small fragile larvae, they must have recourse to at least some reproductive activity in outside waters. Such is evidently the case. The other course, breeding only within the inside "green" waters, can only be specifically successful if some morphologic, developmental or behavioristic habit insures the protection of the young until they are too large to be preyed upon by planktonic elements.

The tarpon has clearly taken the first-mentioned course and only in the "blue" outside waters have larvae of the eggs, that may be those of this species, been taken. None have been taken beyond the size of those reared in the laboratory, the finding of which should lead to their positive or negative identification as tarpon. Clearly this approach to the postlarval tarpon has been no more successful than the attempt of an approach from the larger sizes down, but it does indicate that the larvae developing from this egg, whether tarpon or not, does not move into the estuarine waters as soon as of sufficient size, as do many of the others.

Almost certainly this missing and perhaps off-shore stage is a leptocephalus, as would be expected from general considerations and the fact that the eastern near relative, *Megalops cyprinoides* (Broussonet), has had such a stage identified. Since the leptocephali of this species have been taken in places not unlike the waters well within Pine Island Sound, van Kampen (1909), an intensive search by all methods available to us has been undertaken. This included towing extensively in all manner of likely and unlikely places, dredging the bottom with small fish trawls, using night lights both from docks and afloat and even digging in sandy and muddy places where amphioxus was found. This last examination was instigated by Mr. Stewart Sprin-

ger, who said that he once saw something along with the amphioxys that may have been a leptocephalus. No such specimens were found. After five years of this exploratory effort in both summer and winter, it would seem fair to assume that the leptocephali are not to be found regularly in these inside places.

In attempting to carry on the larvae from the eggs supposed to be those of *Tarpon*, a variety of treatments were given, including reducing the salinity of the water and transfer to fresh water from pools in which young tarpon lived. In none of these experiments was there either an improvement or impairment of viability that could be noted. The latter is the more remarkable since other pelagic eggs similarly treated promptly died. Included in these were *Anchoa*, *Paralichthys*, *Lactophrys* as well as many others not fully identified. Extensive towing in the lower reaches of the Peace River and in numerous ponds produced no such eggs. A single pool, on Captiva Island, into which high surf washed over a low sand ridge, contained both adult *Anchoa* and their eggs, but nothing was seen of the supposed tarpon eggs.

Hildebrand (1934) recorded what he believed to be a young tarpon in the transition from leptocephalus to adult form. Unfortunately this specimen, which was taken at the mouth of Core Creek, Beaufort, North Carolina, was inadvertently destroyed before a figure was made of it, with the result that all that is now available is the brief description given by Hildebrand. There is no reason to suppose that it is not the young of the tarpon, except for a peculiar feature of the fin ray counts. Hildebrand gives dorsal 12 and anal 20. It so happens that these are the counts generally given by taxonomists on adult material, as is shown in Table V. As pointed out in the section on the body proportions of tarpon, in the smaller sizes, of three inches and under, the extra rays are clearly evident. It would seem that surely the counts to be found in a transforming leptocephalus of this species would be, dorsal 15 to 17 and anal 23 to 27. No doubt at this stage and size, 2 cm., some of these rays destined to become consolidated are relatively small, although in the smallest specimens available they actually grade up to the longest ray in each fin. Hildebrand in a personal communication stated that "... the figures given, I am sure, were based on the total number of rays (or fulcra) visible under magnification." This specimen, then, could hardly be the young of the tarpon, unless there is some unexpectedly late development of these elements. The other two possibilities, *Elops saurus* and *Albula vulpes*, are clearly eliminated on the bases of their much different fin counts, as has been

indicated by Hildebrand. The Beaufort region is well out of tarpon country, except as a place for strays to turn up, as also is indicated by Hildebrand. It thus is conceivable that this might equally well be a stray from most any place south of North Carolina and might be referable to some other isospondyle, although what could possibly be a suitable form is not evident. It thus appears that this specimen must rest as a probable, but uncertain, record until more material serves to clarify the fin count matter.

#### JUVENILE TARPON.

Tarpon are next known from fishes from about 5 cm. upwards. The smallest that we have obtained measures 4.2 cm. in standard length. Various features of these sizes are given in Tables I, II, III, VI and X. Table VI indicates the sizes of the small ones that Mr. Bishop actually saw entering a small pool from the open sea. A second small sample taken twelve days later from this same place, then land-locked, suggests that as a group they showed a mean growth of a little over 2 cm. which is not out of line with what one might expect of a species reaching such a large size. The actual growth rates of some individual fish under a variety of conditions is given in Table VII. These are all fully positive records of marked individuals and serve to indicate the response in growth variation that these fishes show to various kinds of environments. It has been long suspected that the tarpon found in small land-locked pools may be stunted. The first part of the table indicates that certain individuals under such conditions may show no growth whatever in periods up to and over five months. In respect to growth these fish are comparable to those kept in aquaria of various sizes, which is in reasonable accord with what one would expect from the evident mean growth of those taken as they entered such places.

In this same table are given calculations of the rates of increment in length, reduced to a standard annual basis, for purposes of comparison with the apparent increase of the fishes measured in Table VI. From this it is clear that the smallest tarpon, evidently just out of the leptocephalus stage, are growing at a relatively terrific rate, but as soon as they reach the size of the smallest otherwise to be found in this pool they drop down to a relatively slow growth. Those kept in the laboratory pool and in small aquaria showed a mean growth of the same sort, while those in the Sanibel pools showed marked stunting, as already mentioned. These relationships are indicated in Text-figure 5.

Larger specimens kept at the old New York Aquarium showed a higher growth

TABLE VI. MEASUREMENTS OF COLLECTIONS OF THE SMALLEST TARPON.

These include the smallest specimens of definite record. They were collected, on the first date, just as they entered a pond on Sanibel Island, from the Sea.

Cm. standard lengths	NUMBER OF SPECIMENS	
	Aug. 8, 1939	Aug. 20, 1939
4.2	1	—
4.9	1	—
5.0	5	—
5.1	1	—
5.2	4	—
5.3	8	—
5.4	8	—
5.5	5	—
5.6	2	—
5.7	5	—
5.8	5	—
5.9	3	—
6.0	2	—
6.1	—	—
6.2	1	—
6.3	—	—
6.4	—	—
6.5	—	—
6.6	—	—
6.7	1	—
6.8	—	—
6.9	—	—
7.0	—	1
7.1	—	—
7.2	—	—
7.3	—	—
7.4	—	3
7.5	—	2
7.6	—	3
7.7	—	2
7.8	—	3
7.9	—	1
8.0	2	2
8.1	—	—
8.2	—	1
8.3	—	2
8.4	—	2
8.5	—	1
8.6	—	—
8.7	—	1
8.8	—	—
8.9	—	—
9.0	1	—
9.1	—	1
9.2	1	—
9.3	—	1
9.4	—	—
9.5	1	—
9.6	—	—
9.7	—	—
9.8	—	1
10.1	1	—
10.6	1	—
11.2	1	—

Date	Maximum	Mean	Minimum
8/8/39	11.2	6.0	4.2
8/20/39	9.8	8.0	7.0
Measurements in cm. total lengths.			
8/8/39	14.7	7.7	5.8
8/20/39	12.7	10.3	8.9

TABLE VII. FULLY POSITIVE RECORDS OF TARPON GROWTH.

All measurements in cm. total length.						
Initial date	Initial length	Final length	Elapsed days	Increment	Growth rate <sup>1</sup>	Tag number
7/11/38	34.5	39.0	258	4.5	18.5	15038
7/20/38	37.0	38.0	167	1.0	5.9	15136
8/ 4/38	36.0	36.0	152	0.0	0.0	15137
8/23/38	35.5	35.5	133	0.0	0.0	15129
8/23/38	36.5	36.5	133	0.0	0.0	15124

The first listed in a small pond two miles north of St. James City, Pine Island, "A" in text-figure 2. The rest in a pond three and one-quarter miles north-west of Point Ybel, Sanibel Island, "B" in text-figure 2.						
3/26/39	24.0	33.0	472	9.0	29.0	13420
3/26/39	28.0	29.3	472	4.2	11.6	13421
3/25/39	23.0	33.6	427	10.6	39.4	13422
3/30/39	35.0	52.9	468	17.9	39.9	13424
12/31/41	43.6	46.5	183	2.9	13.3	—

The above released in the laboratory pool on Palmetto Key on initial date.

LABORATORY SPECIMENS						
At the New York Aquarium						Aquarium no.
9/28/39	9.8	11.7	314	1.9	22.5	1
9/28/39	11.0	12.7	314	1.7	17.9	1
9/28/39	12.0	15.7	314	3.7	35.8	1
9/28/39	14.5	17.5	314	3.0	24.1	1
9/28/39	9.4	11.7	222	2.3	40.2	2
9/28/39	10.6	13.0	314	2.4	26.3	2
9/28/39	11.4	13.5	113	2.1	59.6	2
9/28/39	13.2	16.7	314	3.5	30.8	2
9/28/39	9.5	11.0	314	1.5	18.4	3
9/28/39	10.1	11.5	222	1.4	22.8	3
9/28/39	10.2	12.7	314	2.5	28.5	3
9/28/39	10.8	12.5	314	1.7	18.3	3

The above kept in aquaria of standing sea water, 24" x 12" x 12". Specific gravity 1.024. Temperature 22 to 24° C. Water 10" deep.

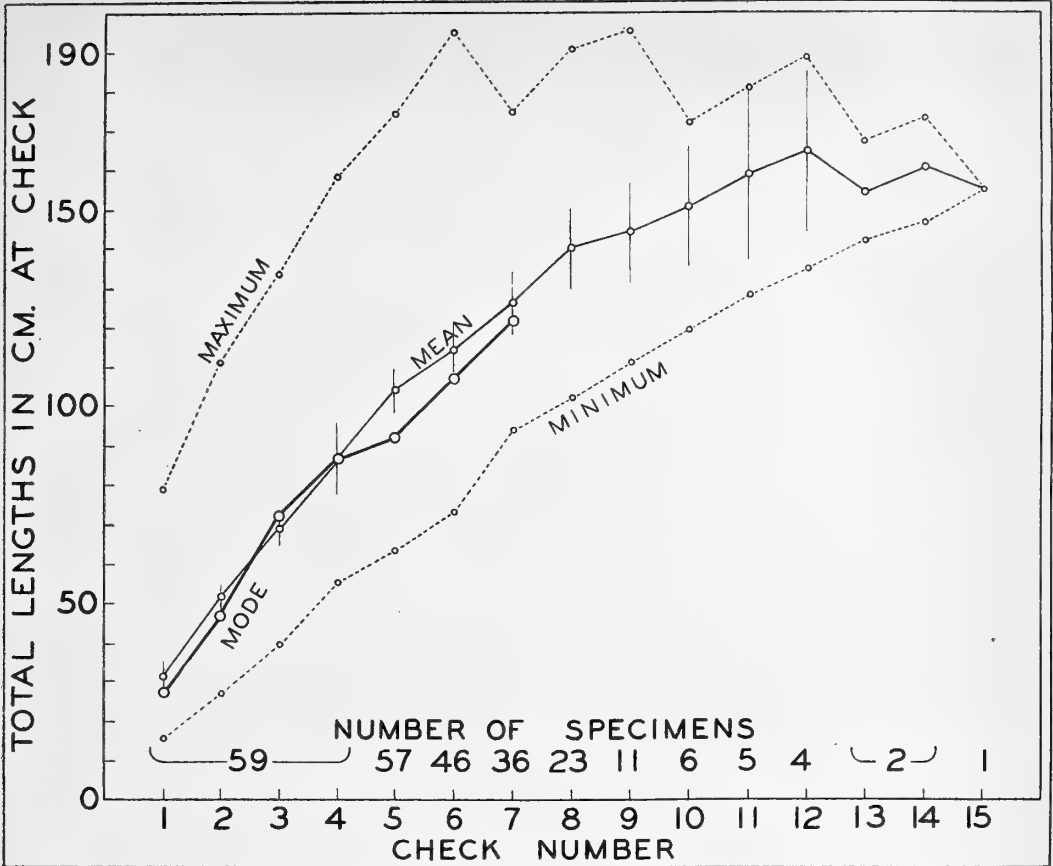
COMPARATIVE GROWTH RATES OF TARPON			
Based on the above fully positive records.			
Location	Number of fish	Mean initial length	Mean growth rate
Pine Island "A"	1	34.5	18.5
Sanibel Island "B"	4	36.2	1.5
Laboratory pool	5	30.7	26.6
Aquarium 1	4	11.8	25.1
Aquarium 2	4	11.2	39.2
Aquarium 3	4	10.2	22.0
All Aquaria (1, 2 & 3)	12	11.1	28.8
Sanibel (newly arrived)		7.7	616.2
(See Table VI)			

<sup>1</sup> Rate calculated as % of increase in total length for one year, according to the following formula:

$$X = \frac{I}{T} \cdot \frac{36500}{L}$$

In which  
L = Initial length  
I = Increment  
T = Elapsed days  
X = Calculated rate of increase





TEXT-FIG. 3. Length of tarpon at the time of development of checks on the scales (annulae?). Based on imprints in celluloid of large scales. The numerical data are given in Table XII. The limits of variation are indicated by the dotted lines marked "Maximum" and "Minimum." Twice the standard error of the means, in both plus and minus directions, is indicated by vertical lines in classes of four or more fish. The number of specimens in each class are indicated below the curve. The values of the mode are indicated by a heavier line than that used for the means down to a lower limit of thirty-six fish below which clear modes could not be established.

rate but still comparable to that of the smaller fish kept in small aquaria and in the laboratory pool. These specimens kept on exhibition at the old New York Aquarium grew from less than 50 cm. up to 122 cm. in a period of five years, see Table XIV. These fish were taken near Key West, Florida. More exact measurements were out of the question because of the demands of exhibition.

The accumulated data of others on the occurrence of small tarpon are given in Table XI. Included with the data of Storey and Perry (1933) is the statement that young tarpon were taken April, 1933, of 8.46 and 12.70 cm. These are not much larger than those we took from another place on Sanibel Island in August at the time of their entry. It may be that these fish had been there a year, as they suggested, but with

the demonstrated lack of growth that sometimes occurs at that place it is possible that they are much older.

#### SCALE ANALYSIS.

The useful method of counting the checks on the scales of fishes as an index of years passed has never been critically investigated in subtropical marine species, although they show markings that could be so interpreted if a sound basis for such a view could be established. In an effort to cast some light on the nature of the checks on tarpon scales, both experimental study and statistical analysis were applied in order to determine if there is any regularity and any statistical significance assignable to these marks.

Certain specimens were taken in land-locked pools, tagged and recaptured at a later date. The data so obtained are given in

TABLE VIII. CHECKS ON THE SCALES OF TARPON ON WHICH THERE ARE FULLY POSITIVE RECORDS OF GROWTH.  
All measurements in cm. total length.  
Scale edges in italics between columns of check calculations.

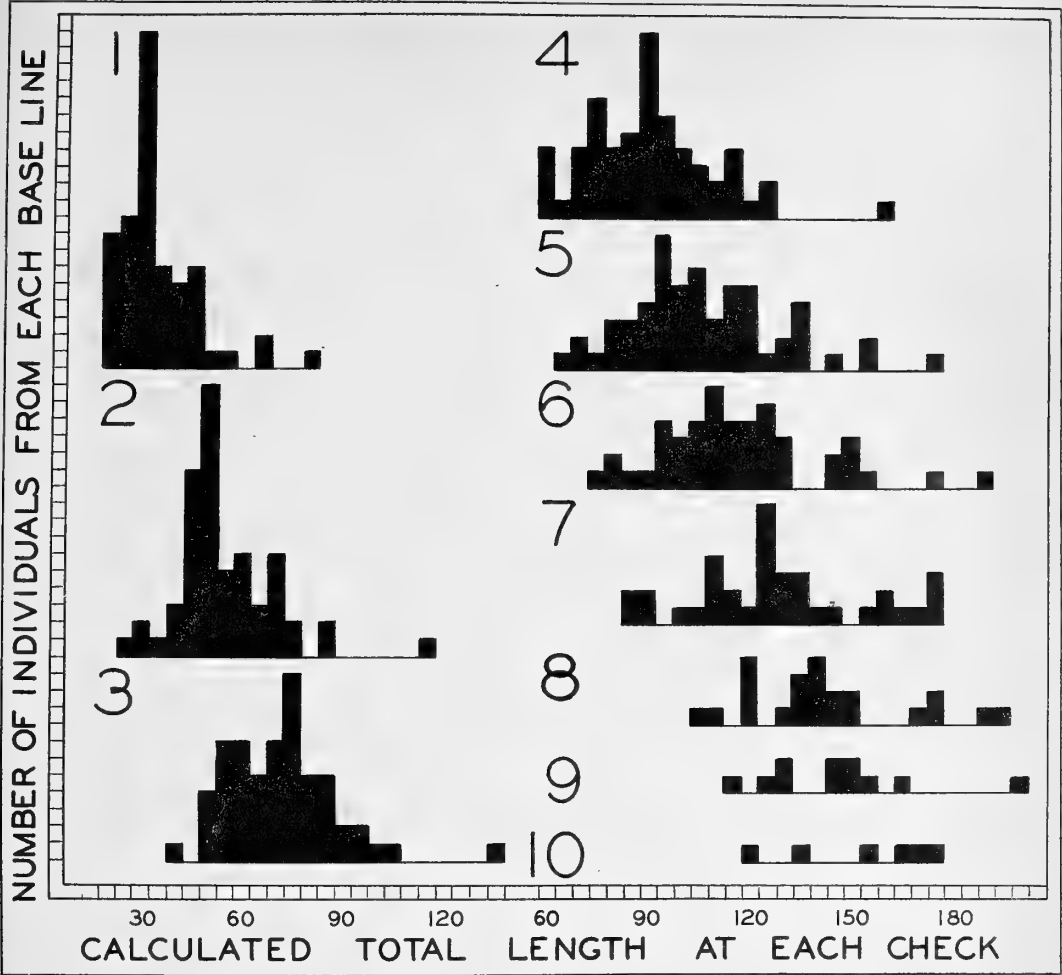
Tag number	Date of scale removal	CALCULATED LENGTH AT CHECK NUMBER:				
		1	2	3	4	5
15038	7/11/38	15.0	22.4	27.5	<i>34.5</i>	
	3/26/39	11.3	21.8	31.8	36.0	<i>39.0</i>
	Mean	<i>13.1</i>	<i>22.1</i>	<i>29.6</i>	<i>36.0</i>	
15136	7/20/38	13.1	19.4	26.2	33.6	<i>37.0</i>
	8/23/38	9.8	16.9	28.4	32.5	<i>37.0</i>
	1/30/39	8.9	17.5	22.8	31.2	35.0 <i>38.0</i>
	Mean	<i>10.6</i>	<i>17.9</i>	<i>25.8</i>	<i>32.4</i>	<i>35.0</i>
15137	8/ 4/38	20.1	30.7	33.4	<i>36.0</i>	
	1/30/39	16.8	26.9	33.5	<i>36.0</i>	
	Mean	<i>18.5</i>	<i>28.8</i>	<i>33.5</i>		
15129	8/23/38	15.1	23.2	25.9	29.8	32.0 <i>35.5</i>
	1/30/39	12.3	21.9	25.4	29.8	32.5 <i>35.5</i>
	Mean	<i>13.7</i>	<i>22.5</i>	<i>25.6</i>	<i>29.8</i>	<i>32.2</i>
15124	8/23/38	11.5	20.4	30.1	33.7	<i>36.5</i>
	1/30/39	11.6	20.1	29.3	32.9	<i>36.5</i>
	Mean	<i>11.5</i>	<i>20.2</i>	<i>29.7</i>	<i>33.3</i>	
L. pool	12/31/41	18.8	31.0	<i>33.6</i>		
	7/ 1/42	18.4	29.5	41.8	<i>46.5</i>	
	Mean	<i>18.6</i>	<i>30.2</i>	<i>41.8</i>		

Table VII. Compared with these data in the same table is similar information on specimens held in aquaria. The markings on the scales of these fishes are given in Tables VIII and IX. Measurements of the markings on the scales of large fish are given in Table XII as proportional parts of the total length of the fish. The total length has been used for this study of the scale markings, as it was found impractical to attempt to induce anglers and others that were kind enough to help, to take measurements in standard lengths. For purposes of conversion Table I, showing the relationship between the total and the standard length, should be consulted.

The values given in Table XII, plotted out according to the number of recognizable checks, are shown in Text-figure 3 on the assumption that they represent some natural regularity in time. The appearance of the mean, maximum and minimum values present a not unreasonable growth curve. Following the methods of Westman and Fahy (1940) and Westman and Gilbert (1941), twice the standard error of the mean is indicated by verticals in both directions. This gives a measure of the significance attached to these values. Large irregularities are no doubt accounted for by the fact that it was impossible to determine the sex in most cases and undoubtedly some of the checks measured are adventitious rings which would make the fish appear older than it was in fact. The excess of the maximum values over the minimum as referred to the mean may be a measure of such sources of error. As a further expression of the extent of the regularity of these check marks,

Text-figure 4 shows histograms of each of the checks of the fishes given in Table XII. The values of these modes is shown in Text-figure 3 comparatively with the mean values and clearly shows substantial agreement. There is thus clearly some distinguishable regularity in time of the formation of these checks. Furthermore they show a regular decrease in spacing with increase in number, which in other and northern fishes is taken to represent the effects of the slowing down of length increment with age in an environment which is responsible for the formation of such checks at uniform intervals of time. The question that then remains is whether this effect on the tarpon scale is in the nature of an annual event or not. This calls for an analysis of changes in the tarpon environment of an annual or other nature.

Most students have hesitated to assign the term annulae to marks on the scales of the more southern species on the basis that the annual change in temperature of the sea or other influences was perhaps insufficient to cause the formation of such checks. Insofar as the fishes of the Florida west coast are concerned, this would seem to be an unwarranted assumption for here in these coastal waters there is a considerable seasonal temperature change. In fact, periodically it drops to lows sufficient to kill large numbers of fishes. See for example Willcox (1887), Brown (1905), Finch (1917), Storey and Gudger (1936), Babcock (1936), Storey (1937). See also Taylor (1917) who discusses other causes of sudden mortality in this region. Gunter (1941) discusses low temperatures on the Texas



TEXT-FIG. 4. Histograms of checks on scales given in Table XII and Text-figure 3, indicating modes, distribution and spread with increasing number. Each class covers 5 cm., the upper limit of which is indicated. The left index indicates units of one fish.

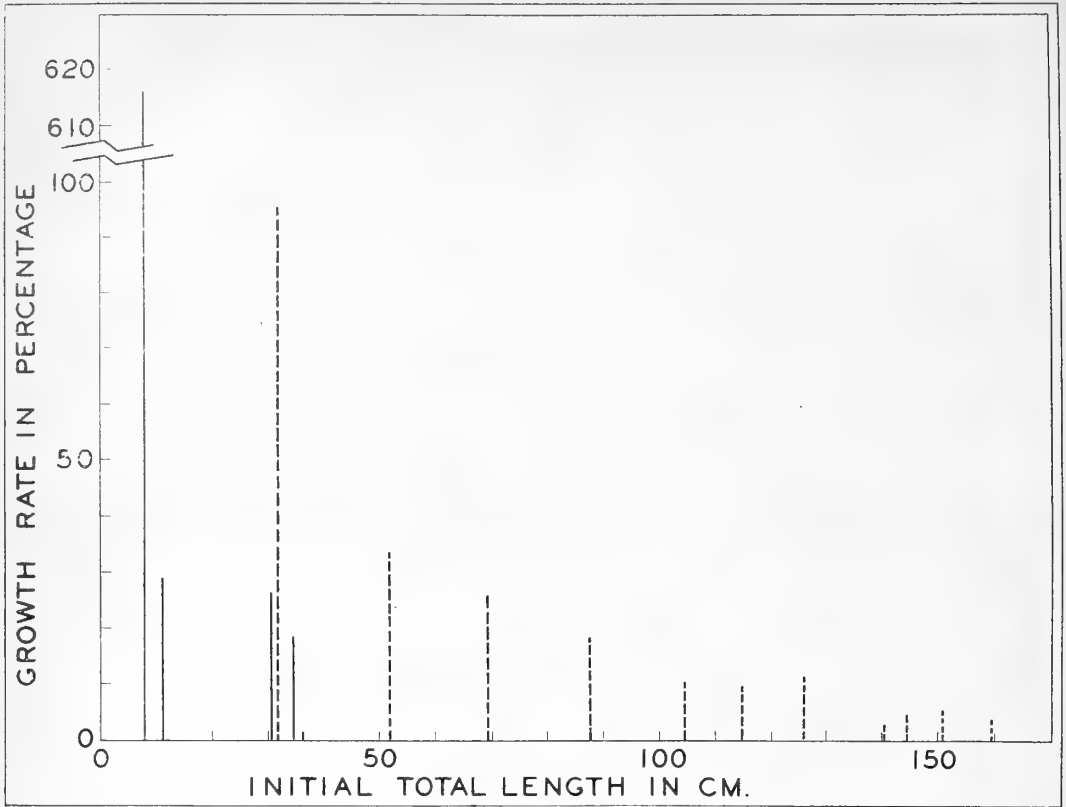
coast bearing on similar matters. Temperature records made at the end of the laboratory dock show the following differences between summer and winter.

TEMPERATURES AT LABORATORY DOCK IN °C.			
	Max.	Mean	Min.
June 4 to July 11, 1940,			
41, 42 (148 readings) ..	33.7	30.8	26.5
March 5 to 31, 1941 (26			
readings) .....	22.2	19.5	15.0

It should be evident from the above tabulation alone that there is a considerable temperature change with the seasons at this place. This is even more marked in backwaters and streams that are much frequented by tarpon. A glance at Text-figure 8 gives some idea of the access of these estuarine waters to the open Gulf at the laboratory site. In addition to simple tem-

perature change there is a large change in the fauna with the seasons. Many fishes are absent or nearly so in winter or summer and the invertebrate faunal change is most striking. It would seem likely that there is a consequently large dietary change with the season, which might influence the whole physiology of the fish.

Other factors that must be reckoned with are those of movements of the fish themselves. There is a considerable movement in and out of streams by these fishes. If there is any regularity to it we have not been able to determine such. At this writing it appears to be entirely sporadic. Local lore is to the effect that tarpon that have been recently in fresh water have a slightly "golden" tinge and that those which have not are "pure silver." Two such color phases are readily distinguished at sight and check



TEXT-FIG. 5. Growth rates of fully positive records of individual tarpon under various conditions compared with the indicated growth rate of large fish according to

the formula 
$$\frac{I}{T} \cdot 36500 = X$$
 based on the data of Tables VI, VII and X. Solid lines, rates of fully positive records. Dotted lines, rates of large fish based on scale readings.

was kept to determine if one showed a predominance at any season. Nothing of such a nature was noted and the two kinds appeared in roughly equal numbers. As many small specimens were kept in aquaria, both fresh and salt, credence is given to this fisherman's belief because those kept in fresh water took on a "brassy" color while those in salt water remained "silvery white." Furthermore it is a common occurrence for many fishes, in passing from salt to fresh water, to lose even more of their bright silvery color and to regain it on returning to the sea, e.g. *Petromyzon* and *Salmo*. This is evidently some physiological matter, perhaps associated with calcium metabolism. If this movement in and out of fresh or nearly fresh water is reflected in the scales, we have no indication of it. Small tarpon can easily withstand a transfer from straight fresh water to sea water of more than normal density or vice versa. Ex-

perimentally they did not throw down a check after such treatment.

Migrations proper, which the tarpon are supposed to make but of which we have as yet no good experimental evidence, would hardly be expected to produce other than "winter rings" in season. The general hypothesis is that they move northward along the Florida west coast and down the Texas coast and back across open waters. Even if this is true they would be exposed annually to a marked temperature differential.

There is thus established the fact that tarpon are exposed to annual fluctuations of temperature of considerable sort, and they cannot be thought of as living continually in an environment of uniform temperature. The above statements refer to tarpon in open waters. Obviously those confined to small land-locked pools suffer even greater extremes of temperature.

In order to attempt to determine if it were justifiable to consider these markings as winter rings, scales of various marked fish were examined at various periods. The results in calculated length at the time the various checks were formed are shown in Table VIII. It will be noted that in each case where a fish passed through a winter, an additional check was formed except in the case of the three fish from Sanibel Island which showed no growth at all and therefore could not form a new check. This table also gives a measure of the extent of accuracy to be expected from measurements and calculations of this kind from tarpon scales. The measurements made on different scales from the same fish, taken at different times, show for most part rather close agreement. The largest deviation from the mean value is in no case greater than 24% and in most cases under 5%.

Growth rates of these measured fish are shown comparatively with similar data from Table XII. Further data of a similar nature on large numbers of small fish are given in Table XIV and the evident growth of these various groups of land-locked specimens is expressed graphically in Text-figure 6. It will be noted that the growth characteristics vary widely from pool to pool and agree with those from which two scale samples had been taken. Compare especially the Pine Island with the Sanibel fishes.

Finally there have been the fishes kept for

several years at the old New York Aquarium. These were held under practically uniform conditions as to temperature and food, in salt water. The data on their growth and scale markings are given in Table XIV and shown graphically in Text-figure 7, compared with the mean values of scales of large fish, taken from Text-figure 3. From this it is obvious that they were growing at a rate comparable with those in the sea. These fish were taken in a body of water open to the sea near Key West and presumably had not been stunted. Two of these, the upper two in Text-figure 7, passed 5 and 4 winters at the Aquarium respectively and showed one check mark for each winter passed. The third, lowest in Text-figure 7, and consequently the smallest, showed 6 checks as against 4 winters passed in the Aquarium. If it is assumed that all had no checks before capture, then it must follow that the checks agree with the number of winters passed through except in the case of one fish that in some way developed two "adventitious" rings. In this connection, when these tarpon arrived at the Aquarium, one died during handling. Its scales were examined for rings and none were found, Breder (1937). Since these markings and the sizes of the fish agree so well with the marks on the scales of large fish, it is difficult not to believe that these marks are in truth winter rings in the ordinary sense of the word. Since, however, the formation of

TABLE IX. DETAILED RECORD OF GROWTH OF CERTAIN INDIVIDUAL SPECIMENS OF TARPON.

All measurements in cm. total length AQUARIUM SPECIMENS (See Table VII)						
Initial date 9/28/39	Second date 113 days	Third date 201 days	First increment	Second increment	Growth rate (1)	Growth rate (2)
9.8	10.5	11.7	0.7	1.2	23.1	20.8
11.0	11.5	12.7	0.5	1.2	14.7	18.9
12.0	14.0	15.7	2.0	1.7	53.8	22.1
14.5	16.0	17.5	1.5	1.5	33.4	17.0
9.4	11.0	11.7 <sup>1</sup>	1.6	0.7	55.0	21.3
10.6	11.3	13.0	0.7	1.7	21.3	27.3
11.4	13.5	—	2.1	—	59.6	—
13.2	15.5	16.7	2.3	1.2	56.3	14.1
9.5	10.5	11.0	1.0	0.5	34.0	8.6
10.1	11.2	11.5 <sup>1</sup>	1.1	0.3	35.2	8.9
10.2	11.5	12.7	1.3	1.2	31.4	18.9
10.8	11.5	12.5	0.7	1.0	20.9	15.8
Maximum					59.6	27.3
Mean					36.6	17.6
Minimum					14.7	8.6

OCCURRENCE OF CHECKS ON SCALES OF ABOVE LISTED FISHES

Date	Number of fish	Number of checks			Total lengths at check number:					
		0	1	2	1		2			
					Max.	Mean	Max.	Mean	Min.	
First	12	7	5	0	12.4	8.9	5.1	—	—	—
Second	11	0	11	0	13.4	9.8	9.1	—	—	—
Third	10	0	8	1	11.8	9.5	8.4	—	13.5	—

<sup>1</sup> Figures marked with footnote 1 in third column represent 109 days instead of 201.

TABLE X. SIZE GROUPS OF TAGGED TARPON BY LOCALITY AND DATE.

Measurements in cm. total length. Modes in 5 cm. intervals—the upper limit indicated.						
LOCALITY	DATE	NO. OF FISH	LENGTHS IN CM.			
			Max.	Mean	Mode	Min.
Pine Island, one to two miles north of St. James City (ditch)	7/ 6/38	32	51.5	34.4	35	27.5
	7/11/38	7	77.4	61.5	65	34.5
	2/26/39	4	61.0	34.0	—	23.0
	3/ 7/39	3	23.5	25.7	—	27.0
Sanibel Island, 1 mile s. of Wulfert (pond)	8/ 9/38	2	66.0	65.5	—	65.0
Sanibel Island, ½ mile s.w. of Point Ybel (ditch)	8/ 2/38	1	—	35.5	—	—
	8/ 4/38	47	48.0	37.1	35	31.0
	8/ 9/38	37	66.5	39.8	35	32.0
	8/25/38	45	49.0	36.5	35	31.0
	3/30/39	5	37.5	35.9	—	35.0
Sanibel Island, 3¼ miles s.w. of Point Ybel (pond)	7/20/38	36	42.5	35.1	40	32.0
	8/ 2/38	54	42.0	35.9	40	32.0
	8/ 4/38	24	38.5	35.8	40	33.0
	8/23/38	46	41.0	36.0	40	31.5
	8/24/38	22	38.5	35.9	40	32.0
	1/30/39	10	38.0	35.6	—	33.5
Boca Grande Island, Railroad ditch 2 miles north of city	6/28/38	1	—	37.5	—	—
	6/30/38	2	66.5	56.7	—	47.0
	7/ 4/38	1	—	58.0	—	—
Captiva Island near Redfish Pass (pond)	8/18/38	1	—	40.0	—	—
Boca Grande Pass	7/ 6/38	3	167.6	144.8	—	127.0
	7/ 7/38	2	187.9	153.6	—	119.4
	7/ 9/38	1	—	152.5	—	—
	3/23/39	2	130.9	122.4	—	113.9
	3/24/39	6	122.0	114.3	—	106.9
	3/28/39	1	—	114.3	—	—
	4/ 4/39	1	—	101.7	—	—
	4/ 9/39	2	167.6	140.9	—	114.3
	4/16/39	1	—	107.8	—	—
	4/20/39	1	—	137.2	—	—
	4/21/39	2	132.2	104.2	—	76.3
	4/22/39	1	—	165.2	—	—
	4/25/39	1	—	183.0	—	—
	4/26/39	1	—	107.8	—	—
	4/28/39	2	183.0	152.4	—	121.9
	4/30/39	3	198.1	183.4	—	156.1
	5/ 1/39	2	152.6	137.3	—	122.0
	5/ 2/39	1	—	122.0	—	—
	5/ 3/39	1	—	137.2	—	—
	5/ 4/39	1	—	152.6	—	—
	5/ 5/39	2	183.0	180.4	—	177.8
	5/ 6/39	2	198.1	152.5	—	106.9
	5/13/39	1	—	137.2	—	—
	5/14/39	1	—	152.5	—	—
	5/18/39	1	—	152.6	—	—
	5/20/39	1	—	127.0	—	—
	5/22/39	2	167.8	155.0	—	142.2
	5/23/39	2	198.1	—	—	183.0
	5/25/39	1	—	183.0	—	—
	5/28/39	1	—	175.2	—	—
	6/ 2/39	1	—	193.2	—	—
	6/ 3/39	1	—	122.0	—	—
	6/ 5/39	1	—	122.0	—	—
	7/28/39	1	—	152.6	—	—
	8/ 7/39	2	177.8	169.9	—	122.0
	8/11/39	1	—	167.8	—	—

TABLE X. (CONTINUED)—SIZE GROUPS OF TAGGED TARPON BY LOCALITY AND DATE.

LOCALITY	DATE	NO. OF FISH	LENGTHS IN CM.			
			Max.	Mean	Mode	Min.
Captiva Pass	7/12/38	1	—	127.0	—	—
	7/13/38	2	137.1	129.5	—	121.9
	7/14/38	1	—	119.5	—	—
	3/26/39	3	137.2	126.3	—	109.3
	4/ 9/39	1	—	139.6	—	—
	5/ 1/39	2	195.7	174.1	—	152.6
	8/ 6/39	2	137.2	129.6	—	122.0
	8/ 9/39	1	—	137.2	—	—
	8/10/39	1	—	101.8	—	—
Redfish Pass	5/15/39	1	—	101.7	—	—
Off Palmetto Key	7/10/39	1	—	137.5	—	—

these rings took place under the abnormally uniform conditions of an aquarium, some source other than some obscure physiological regularity may be sought. The only variable entering into this situation that was not controlled was that of hours of daylight, which is evidently the only item that could account for this situation. As this feature of environment is well established as having similar effects, it may be assumed, subject to further experimentation, that this accounts for the check formation. The fact that electric lights were lighted over the tanks on dark days would be presumably altogether too insignificant to be expected to have any measurable effect. Text-figure 7 also shows the growth of the smallest wild fish of which there is any record; the data of Table VI. This fits nicely with the rest, especially when it is borne in mind that this growth is probably minimal, due to

the fact that these fish were newly trapped on Sanibel Island where it is known that growth is slow or even absent. These data, compared with those already discussed on long term land-locked fish, show clearly that fish from open waters grow at relatively greatly accelerated rates and that there is little in common with the check formations on the scales from the two types of environment. From this it follows that the land-locked forms have little to do with the stock of maturing fishes. No scales from larger fishes have been found that show checks at the small sizes as those from land-locked places. The latter must therefore be looked upon as a peripheral wastage not taking part in the main stock, evidently few escaping from such places to grow up to be large fish, which is in agreement with the opinions of Babcock (1936). Another approach to an attempt to under-

TABLE XI. ACCUMULATED RECORDS OF SMALL TARPON.

AUTHORITY	SIZES IN CM. <sup>1</sup>	LOCALITY	DATE
Evermann & Marsh (1902)	19-29.1 s.l.?	Huacares, Porto Rico	February
Eigenmann (1902 & 1921) <sup>2</sup>	2-19.2 s.l.?	Pinar del Rio, Cuba	March
Coker (1921a)	25 s.l.?	Dauphin Island, Alabama	January
Coker (1921b)	5.7-6.0 s.l.	Fajardo, Porto Rico	-----
Beebe (1927 & 1928) & Beebe & Tee-Van (1928)	5.1-20.3 s. l. 7.6-33.1 s.l. 11.4-17.8 s.l.	Source Matelas, Haiti Source Matelas, Hait Source Matelas, Haiti	January 13 January 23 March 21
Breder (1933)	15.5-28.0 s.l.	Andros Island, Bahamas	February
Storey & Perry (1933)	12-38 s.l.? 8.5-17.7 s.l.?	Sanibel Island, Florida Sanibel Island, Florida	"Any time" April
Babcock (1936) <sup>3</sup>	27.5-47.9 t.l.? 20.3-35 t.l.? 1-4 lbs. small 7.6 t.l.? 25.4 t.l.?	Boca Grande, Florida Shark River, Florida St. James City, Florida Grenada, Jamaica Aransas Pass, Texas Cristobal, Canal Zone	----- February ----- ----- ----- -----
Breder (1937)	circa 15.2-22.8 s.l.	Key West, Florida	June
Breder (1939c) <sup>4</sup>	Upwards from less than 6.0 s.l.	Sanibel Island, Florida	August
Original <sup>5</sup>	31.1-32.4 s.l.	Chagres River, Canal Zone	April

<sup>1</sup>Various measures converted to cm. standard length where practicable.  
<sup>2</sup>The smallest, 2 cm., has never been located as a preserved specimen and there is some question as to whether this is a misprint. See Babcock (1936) for a discussion of this specimen.  
<sup>3</sup>This author quotes and discusses many of these records and those of larger fish.  
<sup>4</sup>Actually 4.2 to 11.2 s.l. See Table VI.  
<sup>5</sup>From data and photographs obtained from Mr. William Markham. Evidently the same location as those of Babcock's Canal Zone records.

TABLE XII. CALCULATIONS OF SIZE AT TIME CHECKS WERE FORMED, BASED ON CELLULOID IMPRINTS OF LARGE TARPON SCALES.

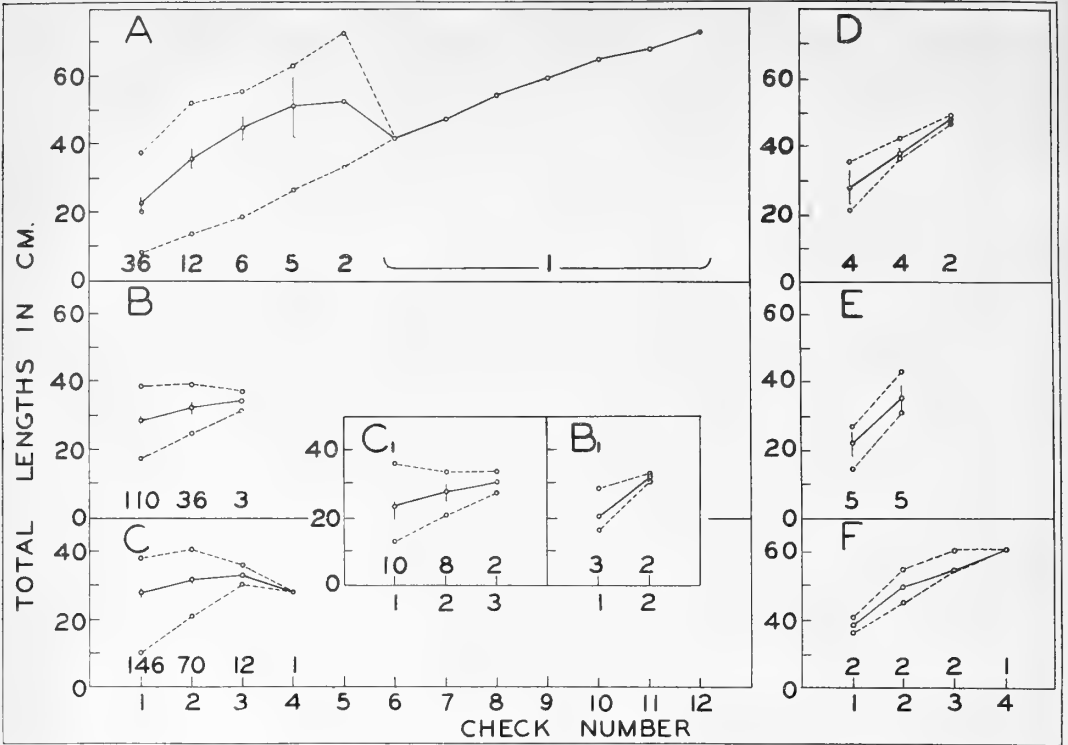
Date collected	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
7/ 3/38	37.6	49.3	71.5	88.0	98.7	111.8	122.0	133.9	147.0	163.2	170.1	178.4	182.0	—	—	—
7/ 6/38	19.6	52.5	72.2	85.3	102.6	117.8	135.3	139.7	—	—	—	—	—	—	—	—
7/ 6/38	21.0	40.6	63.5	81.6	102.0	117.9	127.0	—	—	—	—	—	—	—	—	—
7/11/38	43.5	65.3	87.0	96.8	114.1	129.5	137.4	—	—	—	—	—	—	—	—	—
7/13/38	38.2	61.5	72.6	83.9	94.9	115.5	122.2	—	—	—	—	—	—	—	—	—
7/13/38	37.2	54.3	78.4	99.5	109.5	119.5	—	—	—	—	—	—	—	—	—	—
7/14/38	32.0	40.5	50.1	69.3	77.7	92.8	—	—	—	—	—	—	—	—	—	—
3/23/39	28.4	45.9	72.3	100.7	113.8	—	—	—	—	—	—	—	—	—	—	—
3/23/39	27.5	47.4	63.2	92.5	117.4	130.9	—	—	—	—	—	—	—	—	—	—
3/24/39	27.2	44.5	52.5	64.5	76.5	106.8	—	—	—	—	—	—	—	—	—	—
3/24/39	28.4	49.4	72.8	87.9	98.6	112.7	122.0	—	—	—	—	—	—	—	—	—
3/24/39	42.4	56.9	77.2	89.5	101.7	109.8	122.0	—	—	—	—	—	—	—	—	—
3/24/39	25.8	46.9	75.0	86.7	96.0	105.3	112.4	117.2	121.9	—	—	—	—	—	—	—
3/24/39	16.0	66.7	74.6	88.0	96.0	106.7	—	—	—	—	—	—	—	—	—	—
3/26/39	30.2	45.7	55.9	86.5	104.9	114.1	126.9	137.2	—	—	—	—	—	—	—	—
3/26/39	33.1	45.7	55.9	68.6	88.0	99.3	109.2	—	—	—	—	—	—	—	—	—
3/26/39	30.5	45.7	57.4	66.1	81.3	99.1	104.2	116.9	132.1	—	—	—	—	—	—	—
3/28/39	23.8	40.5	57.1	66.5	78.5	88.0	100.0	111.8	—	—	—	—	—	—	—	—
4/ 3/39	60.8	70.7	79.6	93.9	105.0	108.2	120.5	126.0	—	—	—	—	—	—	—	—
4/ 4/39	23.5	41.2	53.8	70.6	86.4	94.2	101.8	—	—	—	—	—	—	—	—	—
4/ 9/39	19.6	56.8	70.0	96.2	110.7	139.7	—	—	—	—	—	—	—	—	—	—
4/ 9/39	41.8	72.6	97.7	122.8	134.0	145.1	156.2	167.5	—	—	—	—	—	—	—	—
4/ 9/39	29.4	49.1	55.0	70.6	88.3	96.4	105.9	111.9	128.6	137.2	—	—	—	—	—	—
4/20/39	27.8	30.0	47.1	55.7	70.7	83.5	87.9	115.8	132.1	—	—	—	—	—	—	—
4/21/39	26.4	46.3	59.5	72.6	90.2	101.2	110.2	127.6	162.0	172.5	181.2	189.9	198.1	—	—	—
4/23/39	51.2	59.6	68.3	89.5	115.1	121.5	134.2	144.9	162.0	172.5	181.2	189.9	198.1	—	—	—
4/25/39	23.8	38.1	52.8	59.5	69.2	78.6	85.5	102.3	123.8	133.2	142.7	157.0	167.5	173.5	185.4	—
4/27/39	26.2	50.0	71.4	85.6	118.9	150.0	171.2	185.5	—	—	—	—	—	—	—	—
4/28/39	18.7	31.2	53.3	75.1	90.5	103.2	121.9	—	—	—	—	—	—	—	—	—
4/28/39	25.8	55.8	86.1	111.8	129.0	148.3	163.3	172.1	182.9	—	—	—	—	—	—	—
5/ 1/39	43.1	66.3	92.9	112.9	129.2	151.0	166.0	191.0	196.0	204.0	—	—	—	—	—	—
5/ 1/39	42.9	60.2	68.3	85.7	107.0	120.6	132.7	148.7	158.0	—	—	—	—	—	—	—
5/ 1/39	28.8	65.8	78.3	90.6	111.2	127.5	142.0	152.3	—	—	—	—	—	—	—	—
5/ 2/39	22.4	47.4	69.7	102.3	117.0	127.0	—	—	—	—	—	—	—	—	—	—
5/ 2/39	18.2	43.7	58.3	78.2	91.0	105.5	116.3	121.9	—	—	—	—	—	—	—	—
5/ 3/39	25.4	49.7	63.0	73.0	85.2	94.0	108.5	126.0	—	—	—	—	—	—	—	—
5/ 4/39	42.7	51.3	61.2	78.3	91.2	106.9	122.5	135.3	149.5	153.0	—	—	—	—	—	—
5/ 5/39	46.7	80.0	93.5	113.6	133.8	143.8	157.5	170.5	180.4	—	—	—	—	—	—	—
5/ 5/39	64.3	83.5	102.5	118.5	144.2	173.2	182.9	—	—	—	—	—	—	—	—	—
5/13/39	27.4	47.1	80.3	90.1	105.9	119.0	129.4	137.2	—	—	—	—	—	—	—	—
5/14/39	20.8	53.4	72.0	84.6	92.9	104.5	120.8	134.8	144.0	152.3	—	—	—	—	—	—
5/18/39	19.0	42.8	65.6	80.4	93.1	105.8	120.7	139.5	152.3	—	—	—	—	—	—	—
5/18/39	79.4	111.1	133.9	158.8	174.5	195.0	204.0	—	—	—	—	—	—	—	—	—
5/22/39	39.6	65.6	83.9	96.9	111.9	121.2	128.2	137.5	142.4	—	—	—	—	—	—	—
5/23/39	26.5	59.4	83.1	92.3	114.0	123.4	133.0	142.4	152.0	166.2	175.5	182.9	—	—	—	—
5/25/39	25.4	43.8	69.4	92.5	115.7	129.5	153.0	168.9	182.9	—	—	—	—	—	—	—











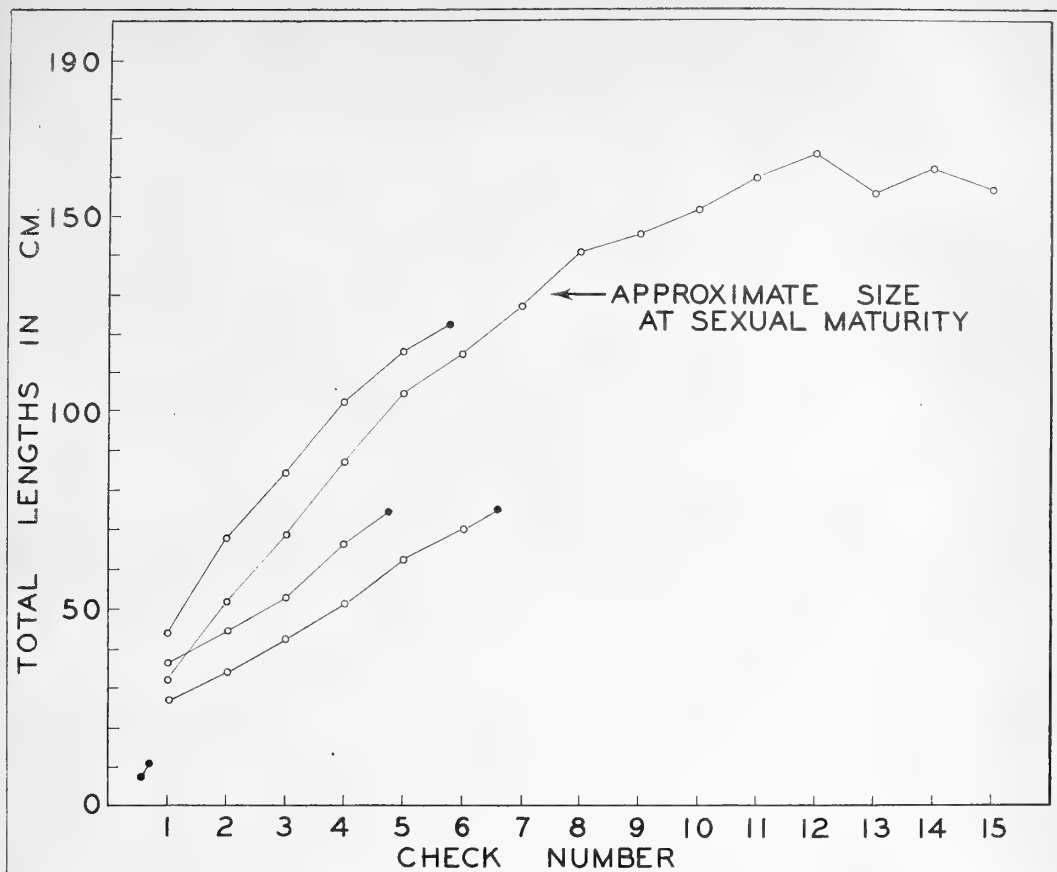
TEXT-FIG. 6. Length of land-locked tarpon at the time of the development of checks on the scales (annulae?). Based on the direct examination of scales. The numerical data are given in Table XIV. Notation as in Text-figure 3. **A.** Pine Island, 1938, and single fish, 1939. **B.** Sanibel Island, ½ mile s.w. Point Ybel, 1938. **B<sub>1</sub>.** Same, 1939. **C.** Sanibel Island, 3 miles s.w. Point Ybel, 1938. **C<sub>1</sub>.** Same, 1939. **D.** Gasparilla Island, 1938. **E.** Laboratory pool, Palmetto Key, 1940. **F.** Sanibel Island, Wulfert, 1938.

were returned by various fishermen to the Government offices by their finders, as shown in the schedule comprising Table XVI.

Recoveries from open waters amount to 5+ % while recoveries from land-locked places amounted to 4- %. Of the former 1+ % represents larger "angler's" fish and 7- % represents small fish which were taken in land-locked places and released in open waters. The details of these data are given in Table XVII.

Since the latest land-locked fish to be recovered had all cast their tags in something over a year, it is to be presumed that the wild ones showed a complete loss in at least the time that has elapsed since then and at present there are no tarpon bearing our tags. A consideration of Table XVI shows that actually the last fish in open waters known to be still bearing its tag was taken 118 days after tagging. Two longer records refer to cast tags picked up on Sanibel beach, while a third is uncertain as to date. The greatest known length of time for a tag to be retained in a land-locked pool is 258 days for tag no. 15038 in Table VII.

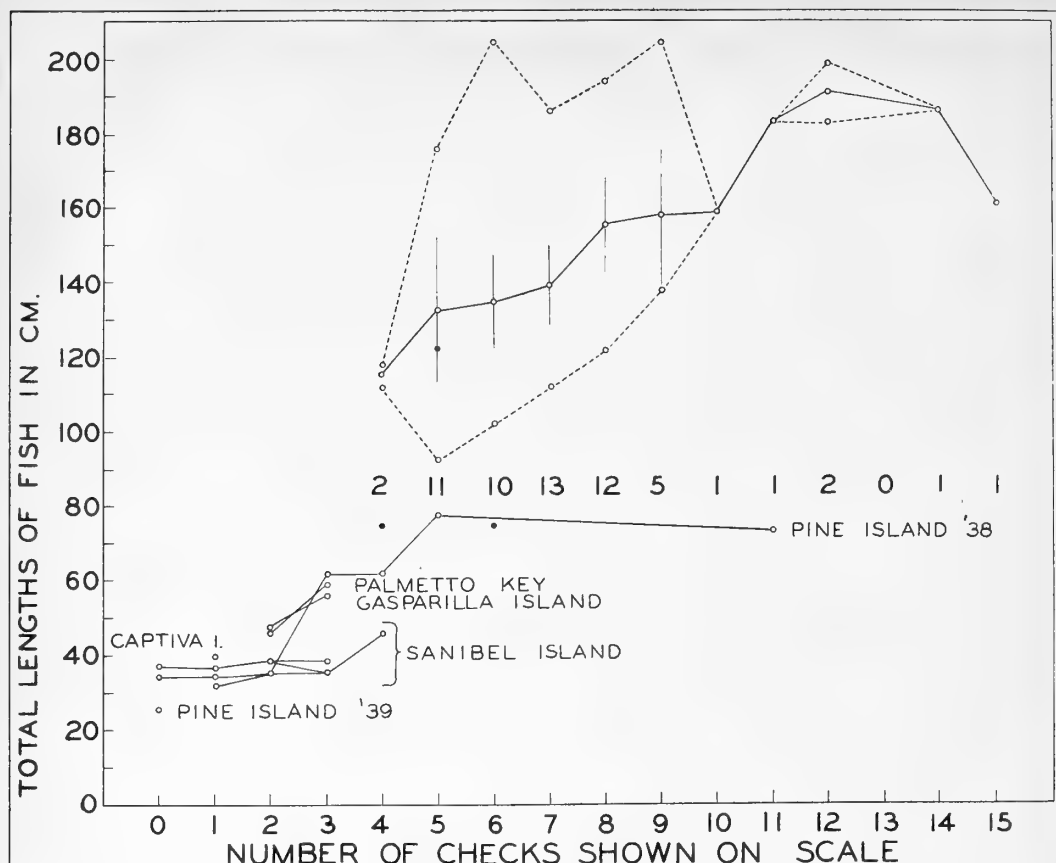
While these data are many too few to base any final conclusions upon, as far as they go they would indicate that retention of either button or strap tags cannot be expected to exceed eight months. Also the loss of tags in pools and the open sea would evidently seem to be about equal in speed. There is no evidence of any unknown intercommunication between the open waters and the supposedly land-locked pools. Such connections are evidently irregularly intermittent due to storms or other changes, as generally supposed. Although most local people and anglers claim that small tarpon are extremely rare, a condition which we did not find borne out in the light of the material collected, we found that all but one of the returns pertained to relatively small tarpon of a size that most people disclaimed any knowledge of ever seeing. Obviously, however, the catchers of these fish must have been angling for other fishes, such as squeteague, for example, or using small seines. That a return of 7- % was obtained by such means would suggest on face value slight loss of tarpons in these size groups incidental to fishing operations



TEXT-FIG. 7. Comparison of known growth of three tarpon in aquaria and the smallest wild fish with the mean values given in Text-figure 3. Numerical data given in Tables VI, XII and XIV. Notation as in Text-figure 3. Dark circles represent measured lengths of fishes and are placed according to date on the assumption that the checks (open circles) represent winters.

for other species. However, since there is such unanimity of opinion concerning the absence of these small sizes, our inability to find such in open waters after prolonged combing of the region would clearly indicate their substantial absence from places frequented by fishermen. It must be recalled that these tagged fish were removed from pools to open water and were thus made available to fishermen by our activities. The low return on the larger fish, 1 out of 77 tagged, would seem to indicate a very small take of the available stock, for here there is a vigorous and active angling fraternity that does catch larger numbers of tarpon in the course of a year, as evidence the records of the hotels at Useppa Island and Boca Grande alone. Consequently there is no indication from this of evidence that the present rate of catch of tarpon as a sportsman's fish is in any way depleting the stock. Furthermore it must be borne in mind that a goodly proportion of the fishes

are released without ever having been fully removed from the water. While the fate of the majority of these is uncertain, undoubtedly a considerable number survive. Suggestive in this connection are the experimental data obtained on laboratory fishes discussed by Schlaifer (1941). Two chief hazards would seem to appear. One, a physiological matter, includes the shock effect so marked on handling tarpon and the amount of success they have in regaining sufficient composure to take the necessary first breath after release. Since most of the tarpon are released in fairly open or deep water and we know the chief hazard to their continued survival at such times to be the proximity of soft flocculent mud, there should not be much loss from this source unless the continued "playing" of the fish or some unknown condition in the large adults or their environment comes into action, working toward their destruction. The second factor involves the presence



TEXT-FIG. 8. Length of tarpon compared with number of checks (annulae?) on scales. From data of Table XIII and XIV. Notation for large fish as in Text-figure 2. The means only are given for the small fish. Fish from Aquarium indicated in solid circles.

of predators in the form of sharks. In the later winter and early spring, sharks are not numerous in Boca Grande and Captiva Passes and probably cut no figure in the matter of any consequence. In the late spring and summer they become exceedingly numerous and voracious. In fact, in the summer it may become almost impossible to land a tarpon, once hooked, because as soon as one gives evidence of being in difficulty, shown by its peculiar swimming movements, the sharks close in, leaving the angler half a fish or only the head. This fact gives some indication of the size and capabilities of these sharks, some of which are easily able to bite through a six- or seven-foot tarpon at one stroke. This condition forced Mr. Bishop to abandon angling in August of both 1938 and 1939 for purposes of tagging. The fish generally become more numerous during that month and many could be hooked, but it was almost impossible to bring any to the boat intact. Consequently it is inferred that early in the year the shark factor

is practically negligible but later nearly completely neutralizes any useful effect that the release of hooked tarpon might have, for during the quarter or half hour period that the tarpon take to recover they would evidently be easy prey to any marauding shark, including those that might not have the courage to strike a hooked tarpon not very distant from a boat.

Although no distinct migratory movement is apparent from these returns, an examination of Text-figure 9 indicates that more were taken to the north of the place of release than to the south, actually 10 to the north and 2 to the south. Expressed in terms of northern distance in miles from the place of release, the captures stand as indicated in Table XVI. It is also evident from these calculations that the group as a whole showed little drift to the west—actually 9 to the west and 3 to the east. The averages of the distances north and west traveled, considering south and east as negative, show that there was a mean drift

of 2.39 miles to the north and a mean drift of 0.29 miles to the west. These fish were all tagged in July or August when local belief has it that the fish are moving north along the coast.

The State of Louisiana, Mathes (1940) reported, started efforts to tag tarpon in that area. Monel strap tags were experimentally affixed to the dorsal fin. This method was earlier tried by us but not put into practice for two reasons. One was the rather discouraging experiences in the past with other species and the other that since much of the tarpon fishing in the Charollette Harbor region is done at night and only the head of the fish brought out of water before releasing, it was felt that a more anterior position for the tags was desirable. There have evidently been no results reported so far from the Louisiana venture.

In connection with the fate of the tags used by us, it was found that the strap tags used either on jaw, operculum, tail, dorsal fin or fleshy part of the back were generally unsatisfactory, tending to set up local irritations, become loose and be shortly cast. The button tags secured to the operculum, two celluloid discs fastened by a pin of pure block tin, did not have such objections if placed well in from the edge. If close to the edge they would frequently tear out. Those that were retained by small land-locked fish would remain for the periods noted, and the external disc frequently became the focus of long, streaming, algae growths, which, however, did not seem to bother the fish in any way. Specimens held in the thoroughly controllable laboratory pool on Palmetto Key, after losing their tags, very quickly healed the perforation so that after a month or so no mark showing the former location of the tag could be found. It is not clear just in what manner the tags were lost. The tin pins seemed perfectly intact on all those recovered. If some corrosive action of environment and physiology is not involved, it is conceivable that the action involved might be entirely mechanical, as the periods of time would give ample opportunity for the exterior disc to become slightly loosened and catch on aquatic growths. The tags were placed firmly against the operculum but there was in no case any evidence of an overgrowth of tissues, the tags remaining completely free at all times.

## DISCUSSION.

The accumulated data on the absence of larval and postlarval tarpon from shore waters indicate that they presumably spend this part of their life history off-shore either in deep or surface waters. In order to determine this, elaborate tow-netting operations from an ocean-going craft would

seem in order. Such a project was planned but the restrictions due to the war time conditions made prosecution impossible. It is hoped to undertake this program as soon as conditions make such activity possible.

The tentative scale analysis indicates that the markings on tarpon probably do indicate numbers of winters passed and that those small specimens taken in land-locked pools are stunted and not part of the perpetuating population. Other estimates of age based on similar specimens have been given by Breder (1933), who found from 2 to 4 checks on land-locked specimens on Andros Island, Bahamas. Coker (1921a) reported no checks on a fish 25 cm. long from open waters in Alabama, and Gill (1907) thought fish of 5.7 to 8.5 cm. in Puerto Rico to be "probably young of the first year." These cases are in keeping with our present findings. Babcock (1936) after much study gives what he calls "little more than a guess" as to the size of tarpon at various ages. Translated to metric measures his values stand as follows:

LENGTH IN CM.	YEARS
30.5— 35.6	1
50.8— 63.5	2
127.0—152.5	3

The growth indicated for the first and second year is in close agreement with our present data as indicated in Text-figures 3 and 7. Since Babcock's "total length" is probably equivalent to our "length including jaw," the agreement is even closer than is at first apparent. The third year is, however, much higher than our indications would call for. The lower estimate is within the present range of extremes but the upper falls without. It would seem that the growth between the second and third year is much too great in Babcock's calculations, for it is more than three times as large as that which he indicates between the first and second. This is obviously a most unlikely condition in practically any growing animal. In another place he indicates that he believes that tarpon of 142.0 cm. may be in their ninth or tenth year, which again agrees closely with our data as indicated in the same Text-figures. This suggests that his figures for the third year are in the nature of some inadvertency of typography.

In all these calculations of the possible age of tarpon, based on scale analysis, it seems to be taken for granted that they form a check the first winter in life. On this we obviously have no data. It has been shown that very small fish do form a check under land-locked conditions but we have no data as to the length of time that is spent as a *leptocephalus*. It may be a very brief period or a very extended one, covering even a year or more. The discussion here

TABLE XV. TARPON TAGGED, BY LOCALITIES AND DATES.

Fish were released at site of capture unless otherwise noted.

DATE	NO. OF FISH	TYPE OF TAG	SERIAL NUMBERS OF TAGS	FISH RELEASED AT
FISH TAKEN IN PONDS AND DITCHES				
PINE ISLAND				
One to two miles north of St. James City. (Ditch).				
7/ 6/38	32	Disc	15004 to 15035.	San Carlos Bay.
7/11/38	7	Disc	15036 to 15039, 15070, 15071, 15073.	—
2/26/39	4	Disc	13420 to 13423.	—
3/ 7/39	3	Disc	13411 to 13413.	—
SANIBEL ISLAND				
One-half mile south of Wulfert. (Pond).				
8/ 9/38	2	Strap	10338, 10339.	—
One-half mile south-west of Point Ybel. (Ditch).				
8/ 2/38	1	Strap	10202.	—
8/ 4/38	47	Strap	10258 to 10267, 10269 to 10284, 10286 to 10288, 10290 to 10291, 10293 to 10308.	—
8/ 9/38	37	Strap	10340 to 10342, 10344 to 10347, 10349 to 10351, 10353 to 10354, 10356 to 10357, 10359 to 10376, 10378 to 10380, 10382 to 10383.	—
8/25/38	20	Disc	15190 to 15195, 15212 to 15221, 15231 to 15234.	—
	25	Disc	15196 to 15211, 15222 to 15230.	South shore of Sanibel.
3/30/39	5	Disc	13424 to 13428.	Laboratory pond, Palmetto.
Three and one-quarter miles south-west of Point Ybel. (Pond).				
7/20/38	10	Disc	15078, 15080 to 15084, 15086, 15090, 15093, 15094.	—
	26	Disc	15095 to 15120.	South shore of Sanibel.
8/ 2/38	54	Strap	10203, 10205 to 10257.	South shore of Sanibel.
	1	Strap	10250.	—
8/ 4/38	7	Strap	10309, 10311, 10312, 10314, 10315, 10335 to 10336.	—
	17	Strap	10316 to 10332.	South shore of Sanibel.
8/23/38	46	Disc	15121 to 15166.	—
8/24/38	22	Disc	15167 to 15184, 15186 to 15189.	South shore of Sanibel.
1/30/39	10	Disc	13400 to 13405, 13407 to 13410.	—
GASPARILLA ISLAND				
Two miles north of Boca Grande. (Railroad ditch).				
6/28/38	1	Disc	15000.	—
6/30/38	2	Disc	15001, 15002.	—
7/ 4/38	1	Disc	15003.	Charlotte harbor.
CAPTIVA ISLAND				
Near Redfish Pass. (Pond).				
8/18/38	1	Strap	10384.	—
FISH TAKEN IN PASSES AND OUTSIDE WATERS				
BOCA GRANDE PASS				
7/ 6/38	3	Disc	15050 to 15052.	—
7/ 7/38	2	Disc	15053, 15054.	—
7/ 9/38	1	Disc	15055.	—
3/23/39	2	Strap	10448, 10450.	—
3/24/39	6	Strap	10401, 10431, 10436, 10440, 10411, 10406.	—
3/28/39	1	Strap	10415.	—
4/ 4/39	1	Strap	10460.	—
4/ 9/39	2	Strap	10408, 10414.	—
4/16/39	1	Strap	10509.	—
4/20/39	1	Strap	10510.	—
4/21/39	2	Strap	10513, 10413.	—
4/22/39	1	Strap	10438.	—
4/25/39	1	Strap	10512.	—
4/26/39	1	Strap	10439.	—
4/28/39	2	Strap	10404, 10405.	—
4/30/39	3	Strap	10519 to 10521.	—
5/ 1/39	2	Strap	10534, 10535.	—
5/ 2/39	1	Strap	10533.	—
5/ 3/39	1	Strap	10488.	—
5/ 4/39	1	Strap	10532.	—



TABLE XV (CONTINUED)—TARPON TAGGED, BY LOCALITIES AND DATES.

DATE	NO. OF FISH	TYPE OF TAG	SERIAL NUMBERS OF TAGS	FISH RELEASED AT
5/ 5/39	2	Strap	10487, 10489.	—
5/ 6/39	2	Strap	10522, 10523.	—
5/13/39	1	Strap	10402.	—
5/14/39	1	Strap	10403.	—
5/18/39	1	Strap	10486.	—
5/20/39	1	Strap	10491.	—
5/22/39	2	Disc	13415, 13416.	—
5/23/39	2	Strap	10466, 10469.	—
5/25/39	1	Strap	10490.	—
5/28/39	1	Strap	10449.	—
6/ 2/39	1	Strap	10476.	—
6/ 3/39	2	Strap	10477, 10531.	—
6/ 5/39	1	Strap	10480.	—
7/28/39	1	Strap	10723.	—
8/ 7/39	2	Strap	10712, 10713.	—
8/11/39	1	Strap	10716.	—
6/18/41	1	Disc	46926.	—
7/ 3/41	3	Disc	46927 to 46929.	Palmetto Key. <sup>1</sup>
CAPTIVA PASS				
7/12/38	1	Disc	15074.	—
7/13/38	2	Disc	15075, 15076.	—
7/14/38	1	Disc	15077.	—
3/26/39	3	Strap	10409, 10441, 10443.	—
4/ 9/39	1	Strap	10506.	—
5/ 1/39	2	Strap	10478, 10479.	—
8/ 6/39	2	Strap	10706, 10707.	—
8/ 9/39	1	Strap	10714.	—
8/10/39	1	Strap	10715 .	—
REDFISH PASS				
5/15/39	1	Strap	10451.	—
PALMETTO KEY				
Off west shore.				
7/10/39	1	Strap	10701.	—

<sup>1</sup> These fish were collected by Mr. M. B. Bishop late in May, and with others were held at the laboratory until

this date of release. They constituted some of the material discussed by Breder (1942e).

as to age is made with this in mind, pending the discovery of the leptocephalus stage and an understanding of its duration.

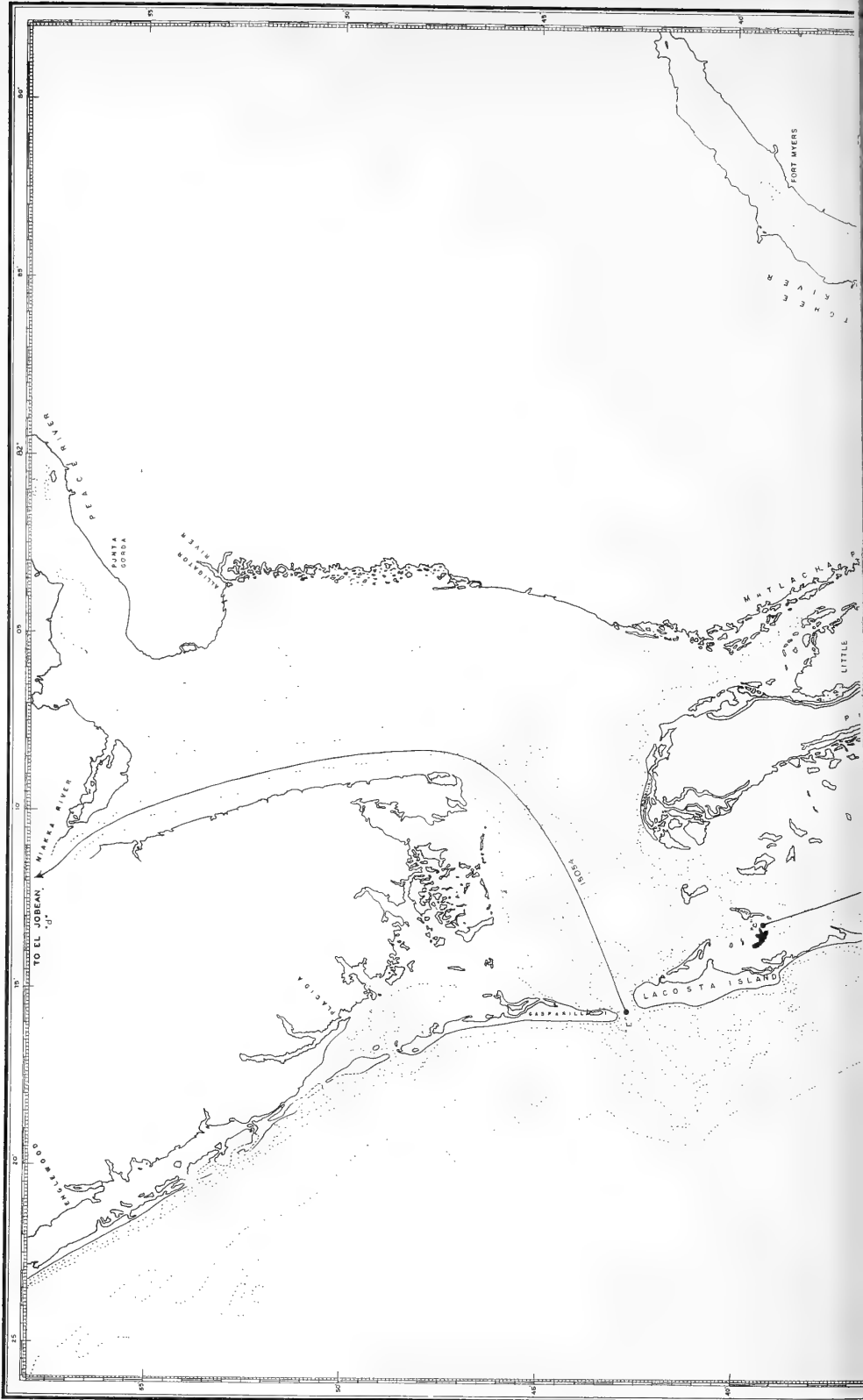
Babcock (1936) gives extended data on the seasons when "angler's" tarpon appear at various places on the Gulf coast. This could be interpreted as a northward migration with the coming of spring, or in various other fashions. The populations may be fairly static without any marked migratory behavior, simply keeping out of sight and not taking anglers' offerings if the water be sufficiently cold. Throughout their range it seems that there are some present at all times and it has been shown that the respiratory rises are less in cold water, as would be expected. This could easily give the impression in the field of comparative absence.

On the other hand, the data on tagging give a suggestion that there may be a slight northward drift of the fishes, but these data are too few to be taken very seriously. This is another matter that cannot be resumed until world conditions become more nearly normal, for tagging at this time could not be expected to produce any

reasonable number of returns with so few people angling.

The assembled data indicate that tarpon may not reach sexual maturity until after passing their sixth or seventh winter. This may be a little too old, for there is still considerable uncertainty about the development of adventitious rings or perhaps spawning checks. In this connection it should be mentioned that in the larger fishes of about this size upward, there were in most cases vague ill-defined bands between the fairly sharp "winter" checks. These were evidently different in nature and placed about half way between the latter. They were not counted in these studies, but it is suspected that they may be spawning marks, which tends to support the general views here expressed. Since tarpon spawn at the warmest time of year and feed actively nearly or quite up to the time of spawning and are ravenous immediately thereafter, it may well account for the diffuse nature of these bands that have been tentatively considered as possible "spawning" checks.

Although tarpon are found on the west coast of Africa, Fowler (1936) and International Game Fish Association (1943),









TEXT-FIG. 9. Chart of region showing deployment of tagged specimens. Based on data of Table XVI. Serial tag numbers, capital letters, at place of release, small letters at place of recovery refer to that table. The connecting lines indicate the short water route. Palmetto Key is indicated in black.

TABLE XVI. RECOVERY OF TARPON, WITH DETAILED DATA ON EACH FISH.  
Measurements in cm. total length.

Tag no.	Tag date	Site of <sup>1</sup> release	Length	Recovery date	Place of <sup>1</sup> recovery	Captor's data	Elapsed <sup>2</sup> days	Statute miles covered		Miles from point of release <sup>3</sup>	
								Dis- tance	Short route	North	West
15006	7/ 6/38	"A"	33.5	10/10/38	"a"	4½ lbs.	96	7.5	9.0	1.48	5.62
15008	7/ 6/38	"A"	27.5	9/ ?/38	"b"	About 15"	56	2.0	2.0	-1.35	0.66
15015	7/ 6/38	"A"	34.0	11/ 1/38	"c"	5 lbs.	118	12.0	17.0	8.35	6.88
15016	7/ 6/38	"A"	38.0	9/19/38	"j"	—	75	7.5	9.0	2.35	-5.62
15054	7/ 6/38	"E"	1193.8	9/17/38	"d"	About 3½'	72	19.0	25.0	14.50	-2.66
15097	7/20/38	"D"	39.0	3/ 5/41	"e"	No fish	228	?	?	—	—
15110	7/20/38	"D"	36.0	10/ ?/38	"f"	—	88	2.5	12.0	1.09	1.09
15116	7/20/38	"D"	38.5	4/ 5/39	"e"	No fish	254	?	?	—	—
10207	8/ 2/38	"D"	38.0	3/ ?/42	"i"	—	1326-?4	2.5	10.5	—	—
10229	8/ 2/38	"D"	35.5	10/ ?/38	"f"	—	75	2.5	12.0	1.09	1.09
10257	8/ 2/38	"D"	33.5	10/ ?/38	"f"	—	75	2.5	12.0	1.09	1.09
10321	8/ 4/38	"D"	37.5	10/ ?/38	"f"	—	73	2.5	12.0	1.09	1.09
10330	8/ 4/38	"D"	33.0	10/ ?/38	"f"	—	73	2.5	12.0	1.09	1.09
15167	8/24/38	"D"	36.0	9/24/38	"h"	1½'	31	11.0	18.0	3.50	3.18
15202	8/25/38	"E"	49.0	10/ ?/38	"g"	5½ lbs.	63	16.5	19.0	-5.57	-10.01
										Mean 2.39	0.29

<sup>1</sup> Letters under "Site of release" and "Place of recovery" refer to the localities indicated in Text-figure 9.  
<sup>2</sup> Italicised dates of recovery and days elapsed refer to date of letter sent by captor where accurate dates were not obtainable.  
<sup>3</sup> South and east expressed as the negative of north and west respectively.  
<sup>4</sup> Presumably this fish was caught much earlier than date of letter. Further information unobtainable.

TABLE XVII. SUMMARY OF ALL TARPON TAGGED.  
Location of Original Capture

NUMBER OF FISH	LOCALITY
<i>Land-locked</i>	
46	Pine Island (1 ditch)
352	Sanibel Island (2 ditches, 2 ponds)
4	Gasparilla Island (1 ditch)
1	Captiva Island (1 pond)
403	All ponds and ditches
<i>Open waters</i>	
61	Boca Grande Pass
14	Captiva Pass
1	Redfish Pass
1	Off Palmetto Key
77	All open waters
480	All fish tagged

PLACES OF RELEASE

Small fish released where tagged, in presumably land-locked pools and ditches..	226
Small fish released in open waters.....	177
Large fish in open waters.....	77
Total .....	480
Total available for retaking in open waters	254
Total available only in ponds and ditches	226

CLASSIFICATION OF RECOVERIES

Numbers retaken in open waters.....	13 <sup>1</sup>
Percentage recovered.....	5+
Numbers retaken in ponds, etc.....	8
Percentage recovered.....	4—
Numbers of large fish retaken.....	1
Percentage recovered.....	1+
Numbers of small fish retaken.....	12
Percentage recovered.....	7—

<sup>1</sup>Omitting 2 tags cast and subsequently found on beach.

and are general throughout the West Indian islands, the coasts of northern South America, Central America and the Gulf of Mexico and do occur in less numbers on the east coast of Florida, they do not occur north of there except as stragglers. At Bermuda they are uncommon, Beebe and Tee-Van (1933). This type of distribution is not uncommon. Whether the Bermuda fish are to be considered as larvae caught in the eastward edge of the Gulf Stream, which have grown up in Bermuda waters, or whether they are accidental strays of larger fish like those that occur irregularly all along the Atlantic coast as far north as Massachusetts, is uncertain, but the indications would seem to be that the larvae are kept, or are able to stay, largely within the Gulf circulation and that it is mainly the larger specimens that have moved outward to form these accidental strays.

SUMMARY.

1. The development of an egg and larva believed to be that of the tarpon is described, down to the pre-leptocephalus stage.
2. Dimensional changes with age and size are discussed and found to be remarkably small, from young to adult specimens.
3. The fate of small land-locked specimens is discussed and the conclusion reached that they are in the nature of peripheral wastage and do not partake in the support of the adult population.
4. The area of successful spawning is considered to be in the blue non-estuarine waters, because of the great abundance of predaceous plankton in the inside green waters.

5. The checks on the scales of tarpon are compared with some of known growth under both wild and captive conditions, which suggests that they are true annulae.
6. Tagging operations suggest that there might be a slight drift to the northward of fishes during the summer months at least.
7. Reproduction is attained at a length approximating four feet in total length, which is also the size of greatest hazard by anglers, but there is nothing in the present data to suggest that the current level or methods of angling is dangerous to the population.
8. Indications are that tarpon become sexually mature after passing their sixth or seventh winter.

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Names in **bold face** indicate new genera, species or varieties; numbers in **bold face** indicate illustrations; numbers in parentheses are the serial numbers of papers containing the Plates listed immediately following.

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\* Dr. Leonard P. Schultz, Curator of Fishes of the United States National Museum, asks that attention be called to "a black 'eye' spot" appearing on the reproductions of *Plate I* in his paper, "Two New Species of Fishes (Gymnotidae, Loricariidae) from Caripito, Venezuela," published as paper No. 5, pages 39-44, in this volume of *Zoologica*. Dr. Schultz states: "This little black spot in the middle of the head must have been added without our knowledge, for it does not appear in the original photograph nor on the fish. The eye is the light area far forward near the tip of the snout."

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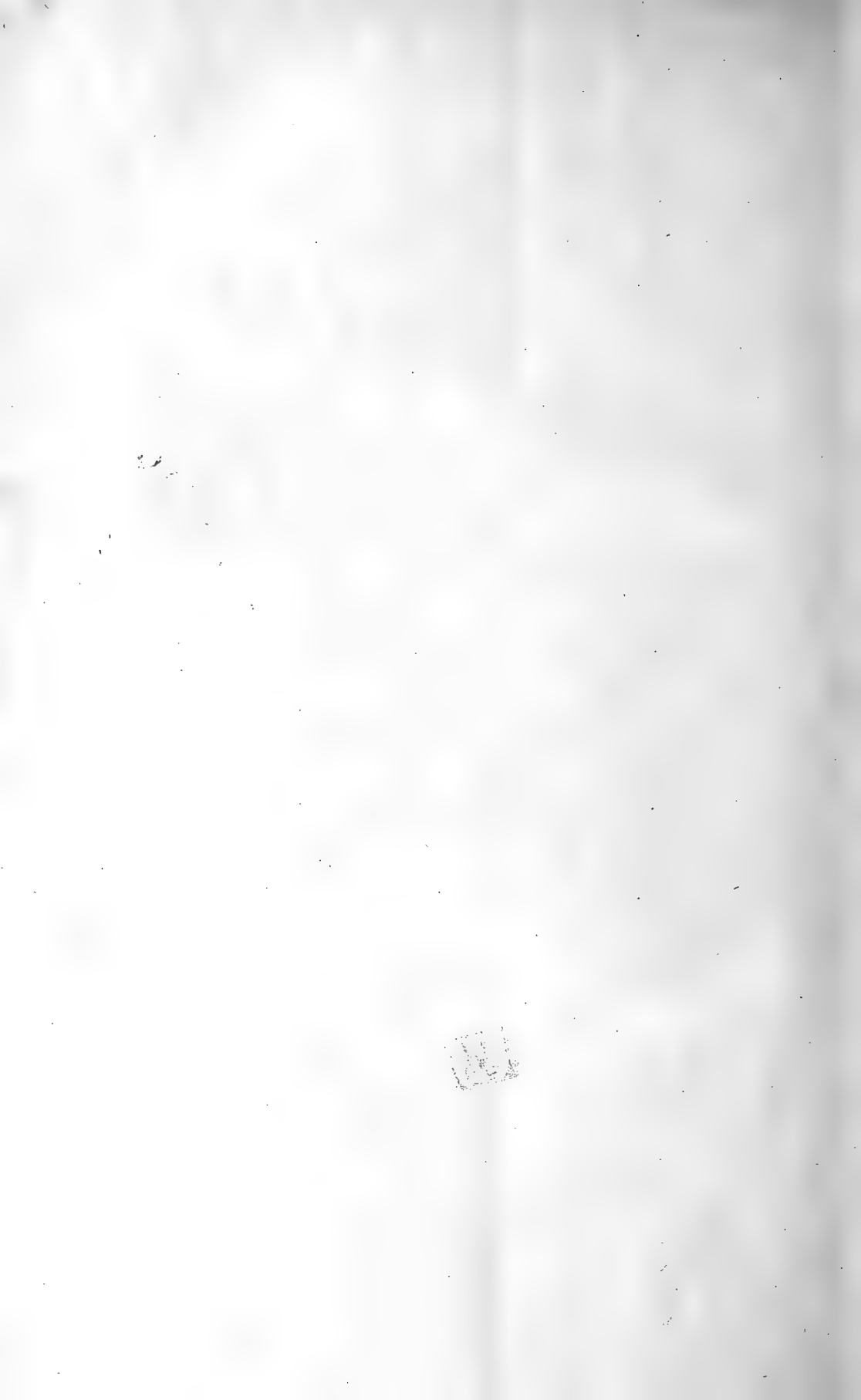
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